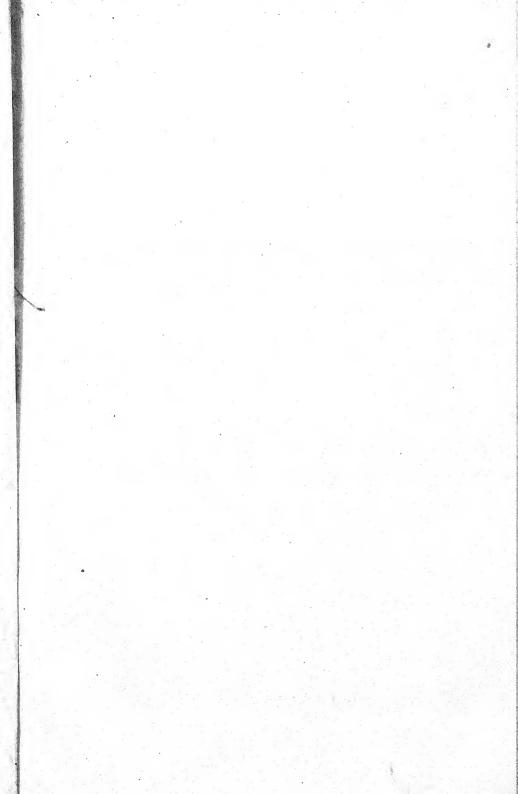
# MYCOLOGIA

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HERBERT H. WHETZEL, PRESIDENT 1939

# **MYCOLOGIA**

OFFICIAL ORGAN OF THE MYCOLOGICAL SOCIETY OF AMERICA

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No. 1

#### GEORGIA PYRENOMYCETES I

JULIAN H. MILLER AND G. E. THOMPSON

(WITH 10 FIGURES)

The fungi discussed in this paper were collected in the spring with mature perithecial stages in or on fallen leaves of the previous season. Types are in the University of Georgia Herbarium, and cotypes have been deposited in The New York Botanical Garden, the Farlow Herbarium at Harvard, and in the Mycological Collections of the Bureau of Plant Industry at Washington.

Several of these organisms possess a dothideaceous type of uniloculate stroma with one-celled ascospores. There is a diversity of opinion among mycologists as to the correct genus for such forms, so a brief review of the history of this question is given below.

The authors wish to express their appreciation to Dr. F. J. Seaver, The New York Botanical Garden, and Dr. D. H. Linder, Harvard University, for the loan of specimens.

#### DISCUSSION OF THE GUIGNARDIA QUESTION

The generic name Carlia was proposed by Rabenhorst (15) in 1857 with the species Oxalidis Rab. as the type. Magnus (10) in 1893 thought Carlia should include Laestadia forms with one-celled ascospores, and so transferred Sphaerella Bidwellii Ellis to Carlia. Von Höhnel (6), on the other hand, says the type Oxalidis is known to equal Mycosphaerella depaseaeformis (Auersw.), and

[Mycologia for November-December (31: 629–754) was issued December 1, 1939] as the latter is a typical Mycosphaerella, all species should be transferred to Carlia.

Sydow (19) cites the original description of Carlia as follows:

"Sphaeriacearum nov. genus, Hormosporae De. N. affine. Perithecia minuta subglobosa e macula prominula. Sporae sphaericae initio toruloidi —concatenatae, episporio crasso, brunneo. Asci nulli."

From the above the fungus is evidently a conidial stage, and so Carlia cannot be used for Laestadia, Guignardia or Mycosphaerella. Clements and Shear (4) recognize this uncertainty and list it among genera dubia.

Laestadia was created by Auerswald (1) in 1869, with Sphaeria alnea Fries as the type. Von Höhnel (6) examines types of the first two species. Laestadia alnea, according to him, grows on alder leaves in patches along veins on the underside, with the perithecia under the epidermis, drying disc shaped, with no ostiole, with a diaporthoid nucleus, no paraphyses, very delicate asci at different levels, and spores with four oil drops probably becoming several celled. He says further this is a Gnomonia without ostiole and without beak, and places it in a new genus, Gnomonina Höhnel. This course is necessary because Laestadia Auersw. is preceded by Laestadia Kunth. (1832), a Compositae genus. He thinks Gnomonina alnea (Fries) Höhnel is related to the Perisporiaceae.

The genus Guignardia was erected by Viala and Ravaz (20) in 1892 with the single species, Sphaerella Bidwellii Ellis, which they named Guignardia Bidwellii (Ellis) Viala & Ravaz. According to von Höhnel (6) they also intended their new genus to include all species of Laestadia Auersw., but they did not realize that Laestadia Auersw. is completely different from Guignardia Bidwellii. He did not examine material of the latter, but says from illustrations it must be a dothideaceous fungus, and that the conidial stages are homologous to ones of Carlia (Mycosphaerella), which should be placed in the Phyllachoraceae. Further, this fungus is a Phyllachora without paraphyses such as Phyllachorella. Guignardia Viala & Ravaz (1892) is hence equal to Phyllachorella Sydow (1914), and therefore the name Laestadia Auersw. cannot be superseded by Guignardia, but must be replaced by Gnomonina Höhnel.

Sydow (19) says it was not the intention of Viala and Ravaz

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to make Sphaerella Bidwellii the type of Guignardia, but to replace Laestadia Auersw. with Guignardia, which would make L. alnea the type. If this is correct then Laestadia—Guignardia—Gnomonina become synonyms, and Clements and Shear (4) so arrange them.

Petrak (11) thinks it will lead to less confusion to accept *Guignardia* with a concept of characters applicable to *Bidwellii* and then emends the genus. His description includes fruiting body with a stromatic wall, small, perithecium-like, with asci more or less parallel, thick-walled, thickened at the apex, 8-spored, paraphyses lacking, and spores short-clavate, or ellipsoidal, hyaline, one-celled.

Lindau (9) describes Guignardia with ascospores at maturity with a cross wall near one end, dividing the spore in two very unequal cells. Ellis (5) does not mention this end cell. Reddick (16), with G. Bidwellii, says to all appearances the ascospores are one-celled, but at one end there is a swollen hyaline vesicle, which he formerly regarded as a second cell. Further, he thinks the spore bears at its extremity a little inflated and transparent mucilaginous material which aids in fixing the spore to the leaf. Von Höhnel (6) says Schroeter describes an end cell, which is entirely wrong, as the spores at maturity remain one-celled. The writers in examining sections of both G. Bidwellii and G. Aesculi (Peck) Stew. find the spores to be one-celled.

Clements and Shear (4) place fungi with characters of *Guignardia Bidwellii*, that is, according to their key, with innate perithecia, not beaked, neither paraphyses nor paraphysoids, and onecelled ascospores, in the genus *Phomatospora* Sacc. As synonyms under this genus they have *Laestadia Auersw.*, *Guignardia* Viala & Ravaz, and *Gnomonina* Höhnel. The type of *Phomatospora* is *P. Berkeleyi* Sacc. (1875).

Saccardo (7) describes the species Berkeleyi from Sphaeria phomatospora Berk. & Br. Von Höhnel (7) examines the type and finds delicate paraphyses, uniseriate, one-celled ascospores, wall of perithecium thin, membranous-leathery, beak spherical to almost cylindrical, and no diaporthoid nucleus. He says it is a Ceratostomella with or without a short beak.

Petrak (12) in describing Phomatospora Filarszkyi, says the

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genus has no genuine paraphyses, but delicate pseudoparaphyses and it stands near the Diaporthaceae. Then later (13) under *Phomatospora moravica*, he says pseudoparaphyses sparse, thread-like, branched, later dissolving, and that the genus is near *Ceratostomella*. According to Petrak then the *Phomatospora* concept is entirely different from that of *Guignardia* with its stromatic fruiting body and no threads in the centrum.

The writers in this paper will follow Petrak in considering

The writers in this paper will follow Petrak in considering *Sphaerella Bidwellii* the type of *Guignardia*, and so restrict the genus to forms with uniloculate stromata, with no beak, fasciculate asci, no paraphyses, and one-celled ascospores.

# 1. Guignardia Bumeliae sp. nov.

Perithecia hypophylla, sparsa, semiimmersa, depresso-globosa, nigra, 92–100  $\times$  104–120  $\mu$ , ostiolo plano, pariete pseudoparenchymate; asci fasciculati, clavati, breviter stipitati, 60–65  $\times$  14–16  $\mu$ , 8-spori; sporae distichae vel inordinatae, ellipticae, utrinque obtusae, continuae, hyalinae, 14–18  $\times$  7.5–9  $\mu$ ; aparaphysata.

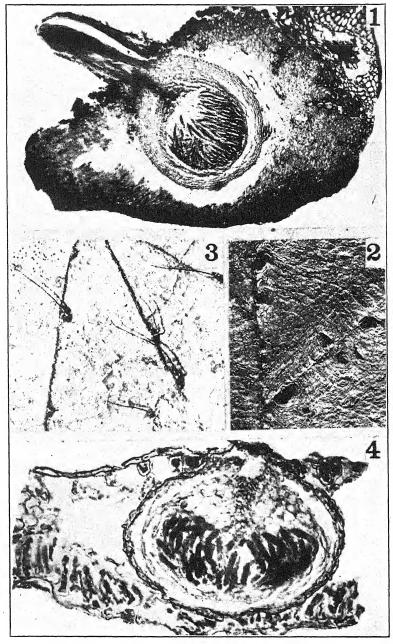
Perithecia chiefly hypophyllous, not in spots, evenly distributed over entire leaf surface, immersed, later partially erumpent, depressed-globose with flat to rounded apices with widely punctiform ostiole, and walls composed of brown pseudoparenchymatous cells,  $10-23~\mu$  thick,  $92-100~\times~104-120~\mu$ ; asci few, fasciculate, arising from a conical basal plectenchyma, clavate, with rounded apices and short stalks, 8-spored,  $60-65~\times~14-16~\mu$ ; spores biseriate to inordinate, broadly ellipsoid with obtuse ends, continuous, hyaline,  $14-18~\times~7.5-9~\mu$ ; no paraphyses. Fig. 10.

On Bumelia lycioides Gaertn., in fallen leaves. Little River, 10 mi. n.w. Milledgeville, Ga. Mar. 20, 1939.

2. Sphaerognomonia carpinea (Fries) Poteb. Ann. Myc. 8: 53. fig. 6-7. 1910.

Sphaeria carpinea Fries, Syst. Myc. 2: 523. 1823. Laestadia carpinea Sacc. Syll. Fung. 1: 426. 1882.

This fungus is interesting in that while it has certain characters closely approaching *G. Bidwellii*, there are other more fundamental ones, especially those of the perithecial centrum, which justify separate genera. It is quite common in Georgia, but it apparently has not found its way into American literature under the above name.



Figs. 1-3. Mamiania Alni; 4, Sphaerognomonia carpinea.

The genus *Sphaerognomonia* was erected by Potebnia (14) in 1910, with *Sphaeria carpinea* Fries as the type. In his figure 6 he shows an uniloculate stroma, with no beak, opening by a break in the tissue over the asci, with more or less parallel-fasciculate asci, each with a ring pore in the apex, and one-celled hyaline ascospores. He says this shows an affinity to *Gnomonia*. The difference is in the lack of a beak.

Von Höhnel (6) says this is *Sphaeria carpinea* Fries and that Potebnia in his figure 6 has shown the asci falsely by having them parallel, and they should have been diaporthoid. Also, this is a *Gnomoniella* with a clypeus and without a beak, and he recognizes the genus *Sphaerognomonia*.

The writers have sectioned material of this species collected on *Carpinus* at Athens, and figure 4 shows a median section. The essential characters are the same as those portrayed by Potebnia's figure. It is an uniloculate stroma and not a true perithecium, the outer wall cells are large with thick, dark-brown walls, while the inner ones are thin-walled and pseudoparenchymatous, and above the stroma is a well marked clypeus in the epidermis. The apex is flat with no beak. The asci arise from the bottom and are more or less fasciculate, and are not diaporthoid in different levels as is true of species of *Diaporthe*, *Valsa*, or *Gnomonia*. They do not fill up the centrum as do those in the perithecium in figure 5. There is definite stromatic tissue above the asci, occupying about one-third of the stroma.

The ostiole is formed in a peculiar manner. When the asci are very young a vertical line of very small meristematic cells, deeply staining, forms in the stroma from a position directly over the center of the asci and continuing through to the surface of the apex. This can be seen in figure 4. The central elements in this line dissolve in the mature perithecium leaving a pore for the discharge of the ascospores. No periphyses were seen in the ostiole, nor were there any paraphyses among the asci even at a very young stage.

There is a very definite ring pore in the apex of the asci as illustrated by Potebnia's figure 7. Also, the asci are short-stalked, easily floating out in water. This fungus then has these diaporthoid characters, but the organization of the wall and the stroma

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sends (ndin) above the asci are indicative of the Dothideales. The writers consider *Sphaerognomonia* as showing more close relationship to *Mycosphaerella* and *Guignardia* than to *Gnomonia*, and it should be so grouped in a natural system. On the other hand it is probable that perithecial forms with the diaporthoid centrum and a well organized wall as *Gnomonia* may have arisen from such a fungus as *Sphaerognomonia carpinea* by the development of an inner organized wall.

The chief separations now between *Guignardia* and *Sphaerog-nomonia* lie in the ascus pore and the floating out of the asci in the latter, and no pore and more or less tightly held asci in the former. Both have one-celled hyaline ascospores, and the asci lie in a stromal cavity.

Sphaerognomonia carpinea has been found in Georgia on the following apparently new hosts: Acer rubrum L., Almus rugosa (DuRoi) Spreng., Betula nigra L., Castanea dentata (Marsh.) Borkh., and Ostrya virginiana K. Koch., as well as on Carpinus caroliniana Walt. Perithecia are found on overwintered leaves in the spring, and are morphologically indistinguishable on the different hosts, but may differ in parasitism as no cross inoculations studies were made.

# 3. Sphaerognomonia polystigma (Ellis & Ev.) comb. nov.

Sphaerella polystigma Ellis & Ev. Bull. Torrey Club 10: 117. 1883.

Anisostomula polystigma Höhnel, Ann. Myc. 16: 49. 1918.

This species has very much the same characters as found in Sphaerognomonia carpinea. The type specimen, N.A.F. 1353, was examined and the stroma opens by the dissolution of a meristematic line above the asci as in the former, and the ascospores have the same measurements,  $10\text{--}12 \times 4\text{--}6\,\mu$ . No morphological characters could be found that warranted its retention as a separate species. However, as conidial stages were not studied nor inoculations made, the writers will temporarily consider it distinct.

Von Höhnel (6) created the genus Anisostomula with Laestadia Cookeana Auersw. as the type, and describes the following distinctive characters: paraphyses numerous at an early stage, later dissolving, asci in one layer, not diaporthoid, no ostiole nor beak,

cross plate in apex of ascus. He follows with a description of Laestadia polystigma which he places in Anisostomula. The writers, on the other hand, found no paraphyses in the type and none in fresh material even at a very early stage, and do find a diaporthoid centrum in that the asci float out in exactly the same manner as in Sphaerognomonia carpinea. Therefore, the fungus on Quercus should be placed in the same genus with the one on Carpinus.

The type of Sphaerognomonia polystigma is on Quercus coccinea Muench. In addition to this oak, it has also been collected in Georgia on the following species which apparently represent new hosts: Quercus alba L., Q. borealis Michx. var. maxima Sarg., Q. cinerea Michx., Q. marilandica Muench., Q. nigra L., Q. palustris Muench., Q. Prinus L., Q. stellata Wang., and Q. velutina Lam.

# 4. Gnomoniella georgiana sp. nov.

Perithecia epiphylla, dispersa, semiglobosa,  $350-450\times220-275\,\mu$ , rostris breviter papillatis, erumpentibus, immersa, pariete coriaceo-membranaceo, brunneo,  $12-20\,\mu$  crasso; asci numerosi, clavati, breviter stipitati,  $69-80\times12-16\,\mu$ , 8-spori; sporae distichae vel inordinatae, oblongo-ellipsoideae, obtusae, hyalinae, continuae,  $15-23\times6-10\,\mu$ ; paraphyses initio evolutae, aetate, omnino mucosae.

Perithecia epiphyllous, irregularly dispersed, slightly depressed-globose, large,  $350\text{--}450 \times 220\text{--}275~\mu$ , entirely immersed in the mesophyll, with short papillate, erumpent ostiola, about  $90\text{--}100~\mu$  high; perithecial walls coriaceous-membranaceous, composed of concentrically arranged very small cells,  $12\text{--}20~\mu$  thick; asci numerous, clavate, with rounded apices, and lower ends attenuated, short stipitate, becoming free in water,  $69\text{--}80 \times 12\text{--}16~\mu$ , 8-spored; spores biseriate to inordinate, oblong-ellipsoid, obtuse, continuous, hyaline, thin-walled, straight or slightly curved,  $15\text{--}23 \times 6\text{--}10~\mu$ ; paraphyses present at an early stage, but gelatinizing at maturity (Fig. 5).

This fungus has a definitely organized wall and a centrum filled with asci that float out in water, which places it in the family Diaporthaceae. The length of the beak is not as long or as filiform as is found in many *Gnomoniella* or *Gnomonia* species, but is about equal to that of *Gnomonia ulmea* (Schw.) Thüm.

On dead leaves both on the ground and on the tree. Type on Nyssa biflora Walt., swamp 7 mi. west Harlem, Ga., Mar. 16,

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1939, also on that species at Towns Creek, Washington Co., Ga., Mar. 20, 1939; on *Nyssa sylvatica* Marsh. Agri. Campus, Athens, Ga., Mar. 21, 1939; on *Liquidambar Styraciflua* L. Agri. Campus, Athens, Ga., Mar. 11, 1939; and 4 mi. southeast of Thomson, Ga., Mar. 16, 1939.

#### 5. Mamiania Alni sp. nov.

Stromata amphigena, sparsa, orbicula vel irregulariter, levia, immersa, superficie atria, intus hyalina, .5–1 mm. in diam.; perithecia solitaria, in centro stromatis, semiglobosa,  $250-276\times295-300\,\mu$ , rostris filiformibus, hypophyllis, 2–7 mm. longis, pariete brunneo, coriaceo-membranaceo,  $35-46\,\mu$  crasso; asci lati, clavato-fusoidei, breviter stipitati,  $57-64\times6.9-13.8\,\mu$ , 8-spori; sporae inordinatae, fusoideo-ellipsoideae, rectae, 1-septatae, leniter constrictae, hyalinae,  $16-23\times4\,\mu$ ; paraphyses paucae, mox mucosae.

Stromata smooth, orbicular to irregular, sparsely dispersed over leaf surface, immersed in the mesophyll, equally visible from both sides, externally black with hyaline interior, .5–1 mm. in diam.; perithecia single in stroma, semiglobose, 250–276  $\times$  285–300  $\mu$ , with brown coriaceous-membranaceous walls, 35–46  $\mu$  thick, with a filiform beak on lower side of leaf, 2–7 mm. long; asci in wall layer, becoming loose in cavity, 8-spored, broadly fusoid-clavate, with short attenuate filiform stalks, 57–64  $\times$  6.9–13.8  $\mu$ ; spores crowded, hyaline, 2-celled but with four oil drops, fusoid-ellipsoid, straight, slightly constricted at septum, 16–23  $\times$  4  $\mu$ ; paraphyses sparse, dissolving into a slimy mass at maturity (FIGS. 1, 2, 3).

The stromata were first seen in dead alder leaves in September, but the perithecia were not mature until the following summer.

On Alnus rugosa (DuRoi) Spreng., Agri. Campus, Athens, Ga., July 5, 1939.

The genus *Mamiania* Cesati & DeNotaris (1863) is based on *Sphaeria fimbriata* Pers. ex Fries. Von Höhnel (8) in a note on *Mamiania*, says the perithecial centrum is typically diaporthoid, and the perithecia are sunken in a white stroma with a black border. These characters fit the above species. Then he further says the spores are very unequally two-celled. The writers do not consider this difference sufficient in this case to provide grounds for a new genus.

The second species described by Cesati and DeNotaris (3) is M. Coryli (Batsch ex Fries) Cesati & DeNotaris, and it has continuous spores, and is the type of von Höhnel's (1.c.) genus, Mamianiella.

This fungus has all of the characters of a *Gnomonia* with the additional one of the stroma. It differs from *Diaporthe* only in that it occurs on leaves and not on wood or bark.

## 6. Ophiodothella leucospila (Berk. & Curt.) comb. nov.

Sphaeria leucospila Berk. & Curt. Grevillea 4: 153. 1876. Linospora leucospila Sacc. Syll. Fung. 2: 357. 1883.

This species was very briefly and inadequately described by Berkeley, and Ellis (5) saw no actual material, but copied the former's description. Since it occurs quite commonly in north Georgia the writers will add the following characterization.

Perithecia hypophyllous in light colored areas along sides of the midrib and chief lateral veins, sunken in mesophyll, under a black epidermal clypeus, with a well organized wall of concentrically arranged cells, which penetrates the clypeus forming a short papilla, with a narrow ostiole; asci cylindric, 8-spored,  $80\text{--}100 \times 4.6~\mu$ ; spores filiform, about as long as the ascus and 1  $\mu$  thick; paraphyses present, tending to disappear with maturity.

This species is placed in *Ophiodothella* because of the lack of an ostiolar beak. The type of *Linospora* is *L. Capreae* (DC.) Fuckel, on *Salix*, and of *Ophiodothella* is *O. atromaculans* P. Henn. Both have perithecia in a pseudostroma and under a distinct clypeus and the beak is the only distinguishing character.

According to Clements and Shear (4) the above species would fall in *Ceuthocarpon* Karst. with no beak. The type is *Linospora populina* (Pers. ex Fries) Schr. on *Populus tremula*, and the specimen on popular leaves (Sydow, Myc. Germ. 249) has distinct beaks on most of the perithecia 250–500  $\mu$  high, and broken ones on the rest, and so *Ceuthocarpon* should be a synonym of *Linospora*.

On overwintered leaves of *Platanus occidentalis* L., Princeton, Ga., Mar. 31, 1939; Tallassee Shoals, Ga., May 1, 1939; and near Sandersville, Ga., Mar. 20, 1939.

# 7. Didymosphaeria Chionanthi sp. nov.

Perithecia hypophylla, dispersa vel aggregata nervisequa, immersa, semi-globosa, rostris breviter papillatis,  $200-250 \times 170-200 \,\mu$ , pariete coriaceo-membranaceo brunneo, ca.  $7-12\,\mu$  crasso; asci clavati, breviter stipitati,  $69-75 \times 10-15\,\mu$ , 8-spori; sporae distichae, oblongo-fusoideae, utrinque obtusae, leniter arctuatae, 1-septatae, plus minus constrictae, dilute brunneae,  $18-22 \times 4-5\,\mu$ ; paraphysoides fibrosae.

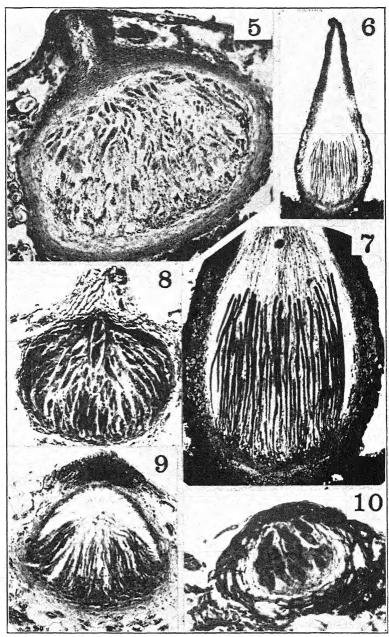


Fig. 5. Gnomoniella georgiana; 6, 7, Acrospermoides subulata; 8, Didymosphaeria Magnoliae; 9, Ophiodothella leucospila; 10, Guignardia Bumeliae.

Perithecia hypophyllous, irregularly scattered, chiefly along the veins, semiglobose,  $200\text{--}250 \times 170\text{--}200 \,\mu$ , with short papillate beaks, immersed in the mesophyll, walls thin and membranaceous,  $7\text{--}12 \,\mu$  thick; asci embedded in thread-like paraphysoids, clavate with attenuate, short stalks,  $60\text{--}75 \times 10\text{--}15 \,\mu$ ; spores biseriate, oblong-fusoid, with obtuse ends, slightly curved, 1-septate, slightly constricted, lower cell somewhat larger than the upper, dilute brown,  $18\text{--}22 \times 4\text{--}5 \,\mu$ .

On dead leaves of *Chionanthus virginicus* L., Little River, 10 mi. northwest of Milledgeville, Ga., May 6, 1939.

#### 8. Didymosphaeria Magnoliae sp. nov.

Perithecia epiphylla, dispersa, immersa vel leniter erumpentia, semiglobosa, apicis papillatis, 138–160  $\times$  115–140  $\mu$ , pariete brunneo pseudoparenchymate, 10–15  $\mu$  crasso; asci lato-clavati, breviter stipitati, 62–74  $\times$  11–14  $\mu$ , 8-spori; sporae distichae, oblongo-fusoideae, rectae vel curvatae, utrinque leniter acutae, 1-septatae, leniter constrictae, dilute olivaceo-brunneae, 18–23  $\times$  4.6–6.9  $\mu$ ; paraphysoides filiformae, ramosae.

Perithecia epiphyllous, sparsely aggregated, immersed, later partially erumpent, semiglobose,  $138-160 \times 115-140 \,\mu$ , with conical papilla,  $40-50 \,\mu$  high, composed of vertical, elongate cells, walls of perithecium brown pseudoparenchymatous,  $10-15 \,\mu$  thick; asci arising from base, embedded in thread-like paraphysoids, broadly clavate, short stipitate,  $62-74 \times 11-14 \,\mu$ , 8-spored; spores biseriate, oblong-fusoid, straight to curved, 1-septate, slightly constricted at the septum, dilute olivaceous-brown,  $18-23 \times 4.6-6.9 \,\mu$  (Fig. 8).

In dead leaves on ground, Magnolia virginiana L., swamp 8 mi. west of Sandersville, Ga., Mar. 20, 1939.

The above two species of *Didymosphaeria* with a stromatic type of wall and paraphysoides attached at the top as well as the bottom of the centrum should be grouped in the Pseudosphaeriales connection.

# Acrospermoides gen. nov.

Perithecia superficialia, globosa-conica, rostris subulatis, atra, pariete membranaceo-coriaceo, levia; asci cylindracei, in paraphysoidibus, 8-spori; ascosporae hyalinae, filiformae.

Perithecia free on substratum, flask-shaped with subulate beak, black, wall membranaceous-coriaceous, smooth; asci cylindric, in paraphysoids, 8-spored; ascospores hyaline, filiform.

#### 9. Acrospermoides subulata sp. nov.

Perithecia hypophylla, superficialia, aequaliter dispersa, atra, globosaconica, rostris, elongato-subulatis,  $380-495 \times 150-185 \,\mu$ , pariete coriaceomembranaceo,  $30-35 \,\mu$ , crasso, exteriore e stratis cellularum atro-brunnearum composito, intus e stratis hyalinis, paraphysoidibus in centro perithecei et in ostiolo; asci cylindracei, basibus attenuatis,  $150-160 \times 4.6 \,\mu$ , 8-spori; sporae filiformae,  $145-163 \times 1 \,\mu$ , hyalinae, continuae.

Perithecia hypophyllous, superficial, uniformly distributed over the leaf surface, black, flask-shaped with elongate beaks, 380–495  $\times$  150–185  $\mu$ , with walls coriaceous-membranaceous, brittle when dry, 30–35  $\mu$  thick, outer cells dark and inner ones hyaline; paraphysoids in perithecial centrum and in ostiole; asci cylindric tapering to stipe-like base, 150–168  $\times$  4.6  $\mu$ , 8-spored; spores filiform, nearly as long as the ascus, 145–163  $\times$  1  $\mu$ , hyaline, continuous (FIG. 6, 7).

On dead leaves, *Morus rubra* L., Agri. Campus, Athens, Ga., Feb. 1, 1939; Princeton, Ga., Mar. 31, 1939; Tallassee Shoals, Ga., Mar. 18, 1939; and Watson Springs, Ga., Mar. 22, 1939.

This species closely approaches Acrospermum in perithecial centrum characters, but differs in the shape of the fruiting body. In the latter it is cylindric to cuneate and terete to compressed, expanding upward, while in Acrospermoides the basal portion is enlarged, tapering to an acuminate apex. Also in Acrospermum the asci extend entirely to the tip, while in this species they attain only about one-third of the perithecial height. In both there are paraphysoids, which would indicate a Pseudosphaeriales connection as pointed out by Brandriff (2) for Acrospermum.

Clements and Shear (4) in the Sphaeriaceae—hyaloscoleciae—have only the genus *Leptosporella* Sacc. as a possibility for perithecia of this type. The type is *L. gregaria* Penz. & Sacc. with spores cylindric-vermiform as illustrated by Saccardo and Penzig (18), pl. 16, fig. 1). This kind of spore is typical of *Lasiosphaeria* Cesati & DeNotaris, and von Höhnel (6) places *Leptosporella* as a synonym under *Thaxteria* Sacc., which he makes a segregate of the older concept of *Lasiosphaeria*.

DEPARTMENT OF PLANT PATHOLOGY UNIVERSITY OF GEORGIA ATHENS, GEORGIA RON

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#### EXPLANATION OF FIGURES

Fig. 1. Mamiania Alni: photomicrograph of cross section of stroma with the single perithecium. This does not include the entire length of the beak. Fig. 2 shows the stromata on the under side of the alder leaf. Fig. 3 is an enlargement of the filiform beaks.

Fig. 4. Sphaerognomonia carpinea: photomicrograph of cross section of leaf with a single stroma. The meristematic layer above the asci, which will become the ostiole, shows very plainly.

Fig. 5. Gnomoniella georgiana: photomicrograph of cross section of a perithecium. The arrangement of the asci is typical of the Diaporthaceae.

Fig. 6. Acrospermoides subulata: photomicrograph of section of perithecium. Fig. 7 is a greater enlargement showing the paraphysoids.

Fig. 8. Didymosphaeria Magnoliae: photomicrograph of cross section of leaf showing perithecium.

Fig. 9. Ophiodothella leucospila: photomicrograph of section of perithecium. This is not exactly through the center, so the ostiole through the the clypeus does not show.

Fig. 10. Guignardia Bumeliae: photomicrograph of section of perithecium. The stromatic wall here is quite different from the organized one in Fig. 5.

## CORDYCEPS SPECIES FROM BRITISH HONDURAS 1

EDWIN B. MAINS

(WITH 2 FIGURES)

As part of an investigation of the biology of the Maya area of Central America, a co-operative study by the University of Michigan and the Carnegie Institution of Washington, the writer and C. L. Lundell spent the summer of 1936 in an investigation of the flora of the El Cayo District of British Honduras.2 The first part of the trip was spent south of the town of El Cayo, mostly at the mahogany camps of Valentin and Cohune Ridge. Short trips were also taken to Retiro and Chalillo Crossing. This area is covered with a luxuriant rain forest. The second portion of the trip was spent in the Mountain Pine Ridge, an area where pine and grasses predominate. Among the fungi collected were a number of interesting species of *Cordyceps* all from the Valentin area. These collections and one received from W. A. Schipp are described and discussed in this paper. Other than the specimen obtained by Mr. Schipp the collections were made by the writer and all are deposited in the Herbarium of the University of Michigan.

#### CORDYCEPS AMAZONICA P. Henn.

Clavae capitate, 1–2 cm. long, the heads ovoid,  $3.5 \times 3$  mm., chestnut-brown, rough from the ostioles, the stipes 1 mm. thick, ochraceous; perithecia ovoid, immersed except for the apices; asci cylindric,  $180-210 \times 4 \mu$ ; ascospores filiform nearly as long as the asci, multiseptate breaking into one celled fragments,  $6-16 \times 1 \mu$  (Fig. 1: A, B).

On cockroaches, Retiro, June 30, 1936 (3688); Cohune Ridge, July 13, 1936 (3838).

Cordyceps Blattae described by Petch (8) on cockroaches dif-

- <sup>1</sup> Papers from the Department of Botany and the Herbarium of the University of Michigan.
- <sup>2</sup> This expedition was aided by funds from the Horace H. Rackham School of Graduate Studies of the University of Michigan.

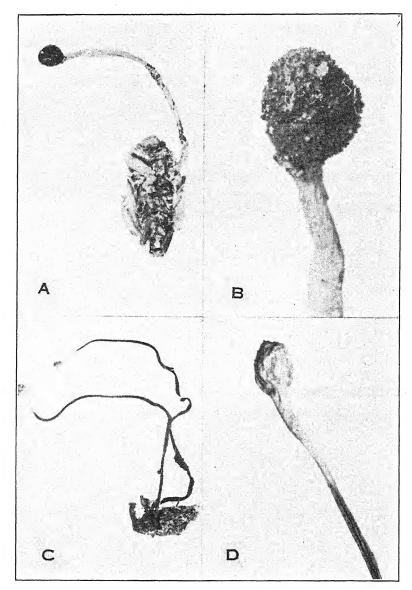


Fig. 1. A, Cordyceps amazonica on cockroach,  $\times$  2; B, head of C. amazonica showing ostioles of embedded perithecia,  $\times$  10; C, Cordyceys curculionum on curculio beetle,  $\times$  2; D, portion of clava of C. curculionum showing bicolored stipe,  $\times$  7.

fers in a number of important respects, specially in having clavate asci and fusoid ascospores. The specimens from British Honduras agree very well with the description given by Hennings (3) for Cordyceps amazonica on Locusta from Brazil. Petch (10) considers C. amazonica the same as C. locustiphila, a species also described by Hennings (3) for Locusta from Brazil. However, both Hennings and Petch describe the fertile portion of the clavae of C. locustiphila as clavate and it would appear doubtful whether the two are the same species.

#### CORDYCEPS CURCULIONUM (Tul.) Sacc.

Clavae arising between the head and thorax, 4–4.5 cm. long, capitate, the heads ovoid,  $1.5-2 \times 1-1.5$  mm., smooth when fresh except for the slightly projecting ostioles, longitudinally irregularly rugose when dried, pinkish-cinnamon when fresh, the stipes 0.5–1.0 mm. thick, black except for 0.5 cm. beneath the head which is concolorous with the head; asci and ascospores not seen (Fig. 1: C, D).

On adult curculio beetle, Valentin, June 29, 1936 (3683).

Although the specimen is immature and data concerning the asci and ascospores are not available, there is no reason for doubting the identity of this specimen. The host and the bicolored clavae distinguish the species. It has been reported a number of times from South America. This is apparently the first report from North America.

#### CORDYCEPS ELONGATA Petch.

Clava bittersweet-orange (Ridgway) when fresh, very slender, 5 cm. long, the stipe 0.8–1.0 mm. thick, yellowish below, brownish-red above (dried), the fertile portion fusoid-clavate, 6 mm. long, 1.5 mm. thick; perithecia reddish-brown, embedded for ½ or  $\frac{2}{3}$  of their height in a soft, orange stroma which shrinks on drying, ovoid,  $250\text{--}300\times200~\mu$ ; asci cylindric,  $250\text{--}300\times4\text{--}6~\mu$ ; ascospores filiform, nearly as long as the asci; breaking into segments  $4\times0.5~\mu$ .

On larva of a lepidopterous insect in a cocoon, Valentin, July 6, 1936 (3766).

This species was described by Petch (11) from specimens collected in Maine and North Carolina. The specimen from British

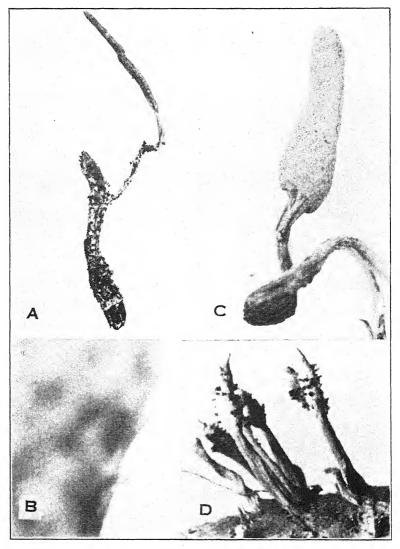


Fig. 2. A, Cordyceps submilitaris on larva of a beetle,  $\times$  1.5; B, portion of clava of C. submilitaris considerably enlarged showing upward projecting ostioles of the oblique perithecia; C, Cordyceps belizensis, head and upper portion of the stipe,  $\times$  2; D, clavae of C. Sphingum developing from between segments of the abdomen of a moth,  $\times$  4.5.

Honduras agrees very well except that the perithecia and asci are somewhat smaller. *C. elongata* resembles *C. militaris* in that the perithecia are partially embedded in a soft stroma. The very slender clavae distinguish it.

#### CORDYCEPS SUBMILITARIS P. Henn.

Clavae brownish-red, cylindric with acute apices, 2–3 cm. long, attached to hosts by orange rhizomorphs, the fertile portion of the clavae  $10-25\times 2$  mm., the stipes 1–1.5 mm. thick; perithecia flattened ovoid or flasked-shaped narrowing to the acute apices, obliquely embedded, pointing upward, the apices projecting; asci cylindric  $300-420\times 3-4~\mu$ ; ascospores filiform nearly as long as the asci,  $0.5~\mu$  wide, obscurely septate, the cells  $2-4~\mu$  long (Fig. 2: A, B).

On large larvae of beetles in rotten logs, Retiro, June 30, 1936 (3686); Cohune Ridge, July 13, 1936 (3836).

This conspicuous species occurs in herbaria under the names, C. submilitaris, C. martialis Speg., C. Lunti Giard (error for C. Hunti Giard 10) C. rubra A. Möll., and C. Klenei Pat. It apparently is a fairly common species of the American tropics.

The larvae are mostly covered with a felt of orange mycelium. The clavae are connected to the larvae by orange rhizomorphs. The clavae vary considerably. As many as six may arise from a larva and in some specimens they reach a length of 5.5 cm. The oblique arrangement of the perithecia is an important diagnostic character.

Whether all the above names should apply is difficult to determine. The earliest name is *C. martialis* published in 1889. Spegazzini (12) describes the perithecia as globulose and makes no mention of an oblique arrangement. Giard (1) also does not describe an oblique arrangement for *C. Hunti* which was published in 1895. *Cordyceps submilitaris* was published by P. Hennings (2) in 1896 based on a specimen collected by Möller in Brazil. Although Hennings does not describe an oblique arrangement Möller (6) states that the perithecia are so arranged. Möller (6) in 1901 described *Cordyceps rubra* with oblique perithecia and this is apparently the same as *C. submilitaris*. Patouillard (7) described *C. Klenei* in 1908. His illustration does not indicate an

oblique arrangement of perithecia. Petch (9) has pointed out that in cross sections of the clavae, oblique perithecia would appear globose and decides that the name *C. martialis* should apply. However until this can be substantiated it seems best to employ the name *C. submilitaris*.

#### Cordyceps belizensis sp. nov.

Clava ochracea, 10 cm. longa, capitulo anguste ovoideo,  $20 \times 9$  mm., stipite 2–3 mm. crasso; peritheciis immersis, ovoideis, 480– $570 \times 260$ – $300 \mu$ ; ascis cylindriceis, 260– $300 \times 6 \mu$ ; ascosporis filiformibus; articulis ascosporarum 4– $8 \times 1.5 \mu$  (FIG. 2: C).

In larva lepidopterae, Retiro, British Honduras, VI, 30, 1936, E. B. Mains (3687).

In the dried specimen the clava is ochraceous. When fresh, the head was antimony-yellow (Ridgway) and the stipe was straw-yellow (Ridgway) stained with red. The head is sharply differentiated from the stipe. It is widest below, narrowing somewhat upward to the obtuse apex. The perithecia are entirely immersed in the stroma which entirely covers the head.

#### CORDYCEPS SPHINGUM (Tul.) Berk. & Curt.

Clavae numerous from various parts of the body of a moth, soft, 7–11 mm. long, the stipes light brown, 0.5–1.0 mm. thick, the fertile portion swelling to 1.5–2.0 mm., whitish, the apices acute; perithecia chestnut-brown, mostly superficial, free, narrowly ovoid, somewhat flattened laterally,  $480-540 \times 180-250 \,\mu$ ; asci cylindric,  $300-360 \times 4 \,\mu$ ; ascospores filiform, nearly as long as the asci; breaking into segments  $4 \times 0.5-1.0 \,\mu$  (Fig. 2: D).

On mature sphinx moth, Camp 36, British Honduras-Guatemala Border Survey, July 15, 1936, W. A. Schipp (\$5959).

This is a very variable species and consequently it has been described under a number of names (5). Sometimes clavae are not formed and the perithecia develop on the mycelial covering of the moth. It is a fairly common species in the tropics and has been collected as far north as New Hampshire.

#### CORDYCEPS VIPERINA Mains

A specimen of this species collected at Cohune Ridge has been reported and described elsewhere (4). It has also been collected in Nova Scotia, Ontario, New York, and Tennessee.

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# A NEW FORM GENUS OF THE MONILIACEAE

DONALD P. LIMBER 1

(WITH 2 FIGURES)

A fungus which, when examined under a hand lens, appeared to belong to the form genus Verticillium was found on the dead roots of a plant of Yucca Treculeana that was of Cuban origin. More detailed study quickly showed the fungus to be distinct. The conidia-bearing branches had a zigzag appearance under low magnification. Under higher magnification they were seen to be similar in form to the rachis of a wheat spike. In this respect the fungus somewhat resembles Polythrincium Trifolii Schmidt & Kunze as described by Wolf.<sup>2</sup> Lacking a perfect stage, its bright yellowish conidiophores and mycelium place it in the form family Moniliaceae and the verticillate habit of the conidiophores assigns it to the tribe Verticilliae. A search of the literature for a verticillate, moniliaceous fungus, bearing conidia on the peculiar zigzag conidiophores described, was unrewarded until our attention was called by Miss Vera K. Charles to a fungus described by Ferraris <sup>8</sup> under the binomial Sporotrichum flavicans Fries var. spicatum Ferraris. This fungus differs from the one under discussion in that it is described and illustrated with conidiophores bearing only a single whorl of branches. We have been unable to secure a specimen of Ferraris' fungus. It was possible, however,

<sup>&</sup>lt;sup>1</sup> Grateful acknowledgment is made to Miss Edith K. Cash of the Division of Mycology and Disease Survey, Bureau of Plant Industry, U. S. Department of Agriculture, who contributed the Latin diagnoses; to Miss Vera K. Charles of the same division for assistance in the search of literature; to Dr. Charles Thom of the Division of Soil Microbiology, B. P. I., for the fungus described under the name *T. album*; and to Mr. John A. Stevenson of the Division of Mycology and Disease Survey, B. P. I., for constructive criticism and assistance throughout the work reported.

<sup>&</sup>lt;sup>2</sup> Wolf, Frederick A. Morphology of *Polythrincium* causing sooty blotch of clover. Mycologia 27: 58-73. illus. 1935.

<sup>&</sup>lt;sup>8</sup> Ferraris, T. Ann. Myc. 10: 295. illus. 1912. Also in: Flora Italica Cryptogama Fasc. 10: 671-672. illus. 1913.

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to grow our fungus on the underside of a cork which was placed in the mouth of a flask of picric acid, thus duplicating the substratum on which S. flavicans var. spicatum was first found. Under these conditions our fungus did not revert to the simpler type of branching described by Ferraris. It seems best, therefore, to describe the fungus isolated from Yucca root as a distinct species.

Though Ferraris described his fungus as a variety of *S. flavicans* it seems clear that he recognized that *S. flavicans* var. *spicatum* bore conidiophores of a form differing from those of the form genus *Sporotrichum* Link. He states, "Curious for the origin of the conidia and the formation of the conidiferous spike. The first conidium is formed at the apex. Below this is formed another branch which bears another conidium somewhat higher up. Thus the first becomes lateral, then there is another branch which extends in an opposite direction, and so always runs alternately, forming a sympodial ramification in the highly regular ensemble. The axis of the spike is accordingly tortuous as if bent zigzag, and is sometimes quite long." <sup>4</sup>

After the Yucca fungus had been under study for about three years, it was our good fortune to receive, through the kindness of Dr. Charles Thom, a similar fungus showing differences of only specific value. On the basis of these fungi and Sporotrichum flavicans Fries var. spicatum Ferraris, the latter of which quite evidently is more closely related to the first two in form than to the genus Sporotrichum and should be transferred to the Verticilliae, we propose the new form genus as described below:

# Tritirachium 5 gen. nov.

Mycelium hyaline or dilutely colored, branched, septate, sinuous, slender; conidiophores long, erect or recumbent, septate, verticillately branched (irregular branching may occur on unfavorable substratum), sometimes biverticillate or triverticillately branched, apical branches slightly subulate at the base and tapering to the rachis-like or zigzag conidia-bearing portion; conidia acropleurogenous, globose to ovate, hyaline or dilutely colored, often conglutinate.

<sup>&</sup>lt;sup>4</sup> Translation from the Italian by Mr. C. R. Sage, specialist in the translation of foreign languages.

<sup>&</sup>lt;sup>5</sup> The name is based on the resemblance in form of the conidiophore tips to the rachis of *Triticum*.

Mycelio hyalino vel pallide flavidulo, ramoso flexuoso, parce septato; conidiophoris longis, erectis vel procumbentibus, septatis, verticillatim ramosis, vel bis vel ter verticillatim ramosis; ramis apicalibus subulatis, alternate in forme rachidis vel "zigzag" ordinatis; conidis acropleurogenis globosis vel ovatis, hyalinis vel pallide flavis saepe conglutinatis.

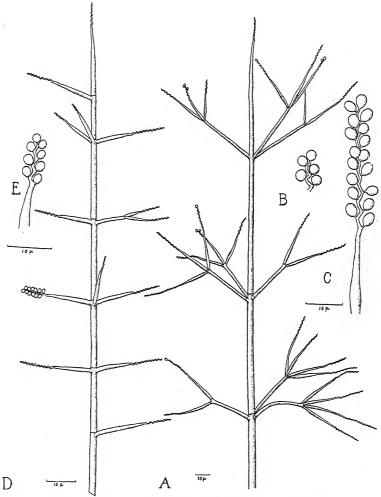


Fig. 1. A-C, Tritirachium dependens; D, E, T. album.

The members of this form genus are readily distinguished from other members of the Moniliaceae by the zigzag form of the fertile portion of the conidiophore (Fig. 2, A, B).

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Tritirachium dependens 6 sp. nov.

Mycelium pale-yellowish to brownish-yellow, branched septate; conidiophores long, stiffly upright, septate,  $2.5-4.8~\mu \times 600-900~\mu$ , verticillately branched; 5-10 whorls of branches, mostly 5; branches in primary whorl 2 or 3, mostly 3, primary branches usually branch giving a secondary verticil of 2-4 branches; secondary branches occasionally branch giving a tertiary verticil; conidiophores and branches cylindric except the terminal branches, these slightly swollen near the base and tapering to the first conidia, from the first conidia to the tip zigzag (Fig. 1, A); a definite spiral can sometimes be detected in young conidiophore tips bearing three or four spores; conidia acropleurogenous, globose to slightly ovate, pale-yellow, smooth,  $2.1-3.3~\mu \times 2.8-3.6~\mu$ , soon cut off, but under favorable conditions spores cohere and may form a club-like mass covering the conidiophore branch or may, on falling away, collect in the axil of the verticil.

Mycelio pallide flavido, ramoso, septato; conidiophoris longis, rigide erectis, septatis, verticillatim ramosis, 2.5– $4.8~\mu$  in diam., 600– $900~\mu$  longis, verticillis primariorum ramorum 5–10, fere 5, praeditis; ramis primariis plerumque verticillum secundarium ramulorum 2–4, et ramulis secundariis interdum verticillum tertiarum gerentibus; conidiophoris et ramis cylindraceis, ramulis spicalibus ad basim subulatis; alternate in forma rachidis vel spiraliter ordinatis; conidiis acropleurogenis, globosis vel aliquanto ovalis, pallide flavis, 2.1– $3.3~\mu \times 2.8$ – $3.6~\mu$ , mox abscissis, saepe circum conidiophorum vel in axe verticilli conglutinatis.

Hab. in radicibus Yuccae Treculeanae, in Cuba, cum Penicillio consociatus.

Type and dried culture deposited in the Mycological Collections of the Bureau of Plant Industry. This specimen is also designated as the type for the genus *Tritirachium*.

#### CULTURAL CHARACTERS

The conidia germinate slowly in agar media. Six to seven days elapse before a single spore colony becomes visible to the unaided eye. Growth on such common media as potato dextrose, corn meal, or lima bean agar is restricted, and in some cultures it is definitely of the starvation type with the aerial growth scant and closely appressed to the surface of the agar. On Thaxter's potato

<sup>&</sup>lt;sup>6</sup> The name refers to the dependence of this fungus on other fungi for accessory growth substances.

<sup>&</sup>lt;sup>7</sup> The conidiophore measurements and details are those of the original interception of *Yucca*. On culture media longer conidiophores are found and more complex branching.

dextrose agar a needle streak spreads laterally only 4–5 mm. (FIG. 2, C, tube labeled control at right). On corn meal agar a needle streak attains a width of 2–3 mm. The color of the aerial growth is "vinaceous fawn" to "avellaneous." Thaxter's potato dextrose agar, used as the substratum, takes on a red color, shading from "garnet brown" to maroon beneath the center of the colony, after prolonged growth of the fungus; when corn meal agar is used, it becomes slightly pink.

Subaerial conidia may be found in cultures grown on corn meal agar. These may occur sparsely, in which case the conidia are few in number on the zigzag branch (1–3) and normal in size; or abundantly. In this case the conidia-bearing portion of the branches resembles a raceme (Fig. 1, C) due to the less crowded arrangement of the conidia and the fact that they are here borne on short sterigma or stalks measuring about 1  $\mu$  long; the conidia are larger, measuring up to 2.3–4  $\mu$  × 3.2–4.5  $\mu$  and are more ovate in shape than the aerial conidia.

#### Tritirachium album sp. nov.

Mycelium hyaline, tortuous, septate, sparingly branched, branches usually near septa,  $1{\text -}2~\mu$  in diameter, conidiophores erect, or recumbent with age, branched, branches usually in whorls of 2–4, occasionally biverticillate with 2–3 branches in secondary verticil, fertile branches short, forming a 70°–90° angle with the conidiophore, sterile portion cylindric to subulate, fertile region zigzag; conidia hyaline, globose or ovate,  $1.6{\text -}2.5~\mu \times 1.7{\text -}3.2~\mu$  (based on 60 measurements).

Mycelio hyalino, tortuoso, septato, parce ramoso, ramis plerumque prope septum,  $1{\text -}2\,\mu$  in diam., conidiophoris rectis vel in maturitate recumbentibus, 2–4 verticilliter ramosis, ramis fertilibus brevibus, parte sterili cylindrica usque subulata, parte fertili "zigzag"; conidiis hyalinis, globosis vel ovatis,  $1.6{\text -}2.5\,\mu \times 1.7{\text -}3.2\,\mu$ 

Dried culture deposited in the Mycological Collections of the Bureau of Plant Industry.

<sup>&</sup>lt;sup>8</sup> Color readings in quotation marks are based on Ridgway. Ridgway, R. Color standards and color nomenclature. 43 pp. Washington, D. C. illus. 1912.

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Fig. 2. A-C, Tritirachium dependens; D, T. album.

#### CULTURAL CHARACTERS

Mycelial mat pure white, forming a low dome or hemisphere, densely matted, covering substrate if moisture conditions remain favorable, surface cottony, margin regular. On Czapek's agar the conidiophores are quite uniformly verticillate (Fig. 1, D) with numerous whorls of short and, usually, simple branches. The color of the substrate on this medium is "orange." On Thaxter's potato dextrose agar vegetative growth is encouraged at the expense of spore production and less regularity is found in the verticillate character of the conidiophores. Fifty per cent of the whorls may be represented by solitary branches. On this medium the color of the substrate is "orange."

This species was received in pure culture from Dr. Charles Thom as acknowledged above. It was separated by Dr. Thom from a colony of *Penicillium intricatum* Thom and was thought to be a contaminant. Dr. Thom received the material from Oscar W. Richards of the Spencer Lens Co., Buffalo, N. Y., who informed the writer that the collection "was taken from a book" in the basement of the Marine Biological Laboratory, Woods Hole, Mass., in 1937. A brief description of this habitat is given by Richards and Hawley. But the reader is cautioned that, as T. album was probably a contaminant of the Penicillium culture, it may have entered the culture at a later date and be of quite different origin. It is perhaps noteworthy that both this species and Tritirachium dependens were found associated with species of Penicillium.

#### SPOROTRICHUM FLAVICANS FRIES VAR. SPICATUM FERRARIS

This fungus is described and illustrated by T. Ferraris as having verticillately branched conidiophores, and zigzag conidiophore tips. As noted above, it resembles T. dependens so closely as to suggest identity. As S. flavicans var. spicatum is not available for study, we are forced to accept the difference in their conidiophore branching, that is, a single whorl of branches, some of which may be forked, for S. flavicans var. spicatum; whereas T. dependens shows many whorls with secondary and tertiary division of the

<sup>9</sup> Richards, Oscar W., & Hawley, K. J. Mold elimination in marine laboratories. Jour. Chem. Educ. 16: 6-10. 1936.

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wuni lindi elf.— branches, as a specific difference. We would assign *Sporotrichum flavicans* Fries var. *spicatum* Ferraris to the new form genus *Tritirachium*.

Tritirachium spicatum (Ferraris) comb. nov.

Sporotrichum flavicans Fries var. spicatum Ferraris.

BUREAU ENTOMOLOGY AND PLANT QUARANTINE, WASHINGTON, D. C.

# EXPLANATION OF FIGURES

Fig. 1, A-C. Tritirachium dependens: A, conidiophore; B, conidia on conidiophore; C, subaerial conidia; D-E, Tritirachium album: D, conidiophore; E, conidia attached.

Fig. 2, A-C. Tritirachium dependens: A, portion of conidiophore with branches; B, conidiophore tip under higher magnification; C, tube labeled "control" shows normal restricted growth on Thaxter's potato dextrose agar; the tubes at the left received additions of growth accessory nature and show a decided response; D, Tritirachium album; tube at left on synthetic media, tube at right on Thaxter's potato dextrose agar. Photomicrographs by Marcel L. F. Foubert.

#### DEVELOPMENT OF GASTERELLA LUTOPHILA

Leva B. Walker <sup>1</sup> (with 45 figures)

Gasterella lutophila was described by S. M. Zeller and Walker<sup>2</sup> from an initial collection of the fungus that had developed upon the surface of saturated woodland loess soil in a greenhouse, during very hot weather. At the suggestion of Dr. Zeller the source of the soil was traced and, as indicated in a note appended to the published paper, abundant additional materials were secured after the paper was in the hands of the publisher. Since then many soil collections from the same region have been obtained during various seasons, and in all cases (except one collection) Gasterella appeared in just three weeks after the soil had been saturated. covered and placed under growing conditions. Soil from this region, on one occasion, was stored dry during the entire summer in a third floor room where the temperatures were near or above 100° F. throughout an especially hot, dry summer. Upon saturation in the fall Gasterella appeared as usual. These later cultures have furnished quantities of materials for study. Soils from other regions that have been tested by the writer have never developed the fungus.3

In spite of the fact that *Gasterella* seems to be so abundantly present in these loess soils the writer or seemingly no one else has been able to find the fungus in its natural habitat. Whether it is epi- or hypogeous in nature is uncertain. Attempts to determine experimentally this point yielded inconclusive evidence. Where

<sup>&</sup>lt;sup>1</sup> Contribution No. 116 from the Department of Botany, University of Nebraska.

<sup>&</sup>lt;sup>2</sup> Zeller, S. M., and Leva B. Walker. *Gasterella*, a new uniloculate Gasteromycete. Mycologia 27: 573-579, 13 figs. 1935.

<sup>&</sup>lt;sup>3</sup> Mr. John B. Routien of Mich. Agr. College writes me he has secured *Gasterella* from several locations in Michigan. A slide sent me agrees perfectly with the original materials studied. His cultures were made during the summer.



the surface of the soil was much roughened the basidiocarps usually appeared most abundantly on the sides of elevations where water stood at the base but in no case where tunnels were made did they become lined with basidiocarps. Light seemed to have little or no effect upon their development. The basidiocarps only developed on saturated soil where the air was saturated also. For this reason it seems probable that in nature these conditions would most readily occur in hollows and burrows such as are characteristic for *Protogaster*.<sup>4</sup>

Many attempts have been made to secure pure cultures of the fungus but spore germination has never been secured and all other efforts have failed. Occasionally bits of soil upon which the young basidiocarps were just beginning to appear gave rise to new growth when transferred to sterilized soil but even this method of propagation was not dependable.

The first evidence of developing basidiocarps of Gasterella is the appearance of tiny tufts of radiating hyphae on the surface of the saturated soil. These tufts enlarge rapidly and within a day or two take on the form of the mature fruit-body. New basidiocarps appear during the next few days but after this brief period additional ones rarely develop. The fruit-bodies when young are snowy white but in a few days they become ashy gray as the darkening spores show through the delicate peridium. When old the walls of the basidiocarps collapse and the fruit-bodies appear under a hand lens much like tiny black cup fungi.

These studies are based upon materials taken from vigorously growing cultures and fixed largely in formol-acetic-alcohol solutions, as these seemed to give the best results. The fixed materials were imbedded in paraffin and sectioned in the usual manner. The most satisfactory stain used for sections was Heidenhain's iron-alum-haematoxylin counterstained with Orange G in clove oil.

<sup>&</sup>lt;sup>4</sup> Zeller, S. M. *Protogaster*, representing a new order of Gasteromycetes, Ann. Missouri Bot. Gard. 21: 231–240. 1934.

<sup>&</sup>lt;sup>5</sup> In the original collection the fact that new basidiocarps failed to develop was erroneously attributed to the very hot weather since all subsequent cultures have behaved similarly.

<sup>&</sup>lt;sup>6</sup> The two formulae used most are (a) neutral formalin 10 cc., glacial acetic acid 5 cc., and 50 per cent alcohol 100 cc., and (b) neutral formalin 6 cc., glacial acetic acid 1 cc., and 50 per cent alcohol 93 cc.

### ORIGIN AND DEVELOPMENT OF BASIDIOCARP

As previously noted, the first appearance of a basidiocarp is the appearance of a tiny tuft of hyphae which radiate from a tangle of hyphae. The youngest of these knots sectioned is shown in figure 2 and more highly magnified in figures 3 and 21. In this as well as other young stages the radiating superficial hyphae are disarranged and intertangled from handling. The first differentiation in the hyphal mass is the appearance of downward growing hyphal tips which form a palisade layer in the upper part of the young knot. This layer is interrupted by undifferentiated primordial hyphae that extend from tip to base through a chamber that is being formed by the expansion due to the developing palisade layer and resultant breaking of the primordial tissue below. Figure 21 is a diagrammatic drawing of this basidiocarp and figure 22 shows a portion of this palisade layer enlarged. The hyphae making up the young basidiocarp are binucleate. Many basidiocarps only slightly older than this one were observed, three of which are shown in figures 4, 5-7, 23-24. As is evident from these figures, the palisade layer broadens laterally and extends downward lining the sides of the enlarging chamber. The individual cells of this expanding palisade layer are enlarging and some appear definitely to be young basidia. At the base of the young basidiocarp the hyphal cells enlarge and coalesce to form a somewhat pseudoparenchymatic base from which hyphae below spread into the substratum. Figure 4, of which all sections were slightly diagonally cut, is probably the next to youngest fruit-body sectioned and shows only a beginning of this pseudoparenchymatic base. The basidiocarp shown in figures 23 and 24 shows clearly the structure when only slightly older. Very often so much dirt is held in this region that it is badly torn or broken away during sectioning. This was true in the fruit-body shown in figures 5-7, where the base is lacking in median sections such as figure 7. Above this pseudoparenchymatic base a few hyphae with scanty protoplasmic content extend out to and through the palisade layer, connecting with the tissue above (FIGS. 23, 24). It is obvious that the palisade-like layer is the young hymenium and that new elements are being added from the meristematic sub-



Figs. 1-20.

hymenial cells to the outside of this layer. The elements in the hymenium and subhymenium are about twice as large in the basidiocarp shown in figures 23 and 24 as in the very youngest knot, figures 21 and 22. The subhymenium merges into the delicate hyphae that will constitute the peridium.

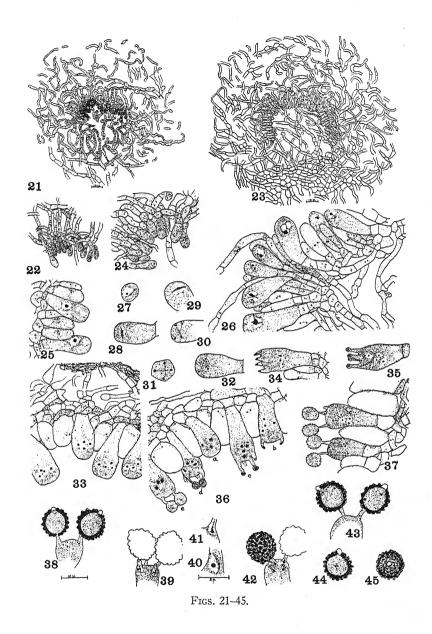
As new elements are added to the hymenium, it becomes arched upward and the primordial hyphae that originally stretched across the central region become broken and remain only as remnants. In this way the single locule characteristic of the fungus is formed. As the hymenium increases in extent it never entirely closes over the gap at the base of the fruit-body (FIGS. 7, 8, 9, 11, 14). This sterile region is usually quite conspicuous but occasionally it is restricted to a very narrow region as in the fruit-body shown in figures 9 and 10. In the border region, between hymenium and the ruptured primordial hyphae at the base depauperate cells, shaped much like basidia, commonly occur. These may be best observed in slightly tangential sections of basidiocarps (FIGS. 5, 6). In this basidiocarp all basidia are still binucleate.

The hymenium seemingly may continue to develop almost indefinitely if growing conditions are favorable or may mature without farther expansion. Very small mature fruit-bodies, formed in exceptionally hot weather, as figures 16 and 17, may show no farther expansion of the hymenium or only a very slight folding at the base. In most of the basidiocarps, however, the hymenium expands so extensively that considerable hymenial folding results. A beginning of this folding is shown in figure 6. Where only slight folding occurs it is usually limited to an area just above the sterile region at the base, figure 8. (Figures 1, 2, and 9 in the published description of Gasterella are in reality slightly tangential and not truly vertical sections taken at the point of greatest diameter. The fold at the base was a lateral fold at one side of the sterile base. The sterile region was mistaken for a break in sectioning.) When conditions are very favorable folding may take place from any portion of the hymenium. Basidiocarps with only uninucleate and young binucleate basidia were observed that were as large and as much folded as the one shown in median section in figure 11 and tangential section in figure 12 and in all intermediate types as figures 9-10, 14-15. As the hymenium expands the peridium stretches out and without modification becomes the delicate cobwebby covering of the mature basidiocarp (FIGS. 9–19). When hymenial expansion ceases the hymenium rapidly matures regardless of the size of the basidiocarp and the extent of folding of the hymenium.

#### DEVELOPMENT OF THE HYMENIUM

As previously stated, the hymenium has its origin in a palisadelike layer that develops in the upper portion of a primordial knot of hyphae. This layer has its origin from downward growing hyphal branches (FIGS. 21, 22). The slightly enlarged hyphal tips and the hyphae from which they originate are all binucleate and very densely filled with cytoplasm. In a slightly older fruit-body, such as shown in figures 23 and 24, the only notable change is the great increase in the size of the elements forming the hymenium and subhymenium. As the individual elements of the hymenium continue enlargement one can easily distinguish three types of cells (FIG. 25): cells in which the two nuceli previously present have fused, basidia; binucleate cells with scanty cytoplasm and large vacuoles, young paraphyses; and binucleate cells with denser protoplasm which are probably young basidia or which have not at least become definitely specialized. The changes indicated here show more clearly in slightly older basidiocarps such as are illustrated in figure 26. Here the basidia are shown as they appear just before meiosis. The paraphyses still retain a clavate shape much like that of the basidia. In this figure, as well as in figures 22 and 24, the remains of primordial hyphae extending through the hymenium are shown. In later stages they are rarely seen.

Meiosis in the basidia seems entirely normal but no attempt was made to determine the details. Three stages of the first division are shown in figures 27–29 and the telophases of the second division in figures 30 and 31. Following the second division four nuclei are organized (Figs. 32, 33). By this time the basidia have reached their maximum size and protrude far beyond the paraphyses which have broadened greatly and contain two small nuclei, scanty cytoplasm, and a very large vacuole. In the basidia the basal region is vacuolate and the nuclei and cytoplasm largely con-



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fined to the upper half of the basidium. A basidiocarp at this age is shown in figures 9 and 10.

Soon sterigmata begin to appear, first as tiny elevations containing a deeply staining granule at their tip. They soon reach conditions such as shown in figures 34 and 35. Successive stages as shown in figures 32-35 may often be observed in a single basidiocarp such as the one shown in median and tangential sections in figures 11 and 12. Figure 13 is a higher magnification of the lower lefthand portion of the fruit-body shown in figure 11. Figure 36 shows the details of a portion of the hymenium in this basidiocarp. a-e representing successive developmental stages as seen in a small area of hymenium. Echinulations are beginning to appear on the walls of the spores developing at the ends of sterigmata on the oldest basidia in this fruit-body as shown in figure 36, e. The development of the sterigmata and spore initials must progress rapidly, because in only slightly older basidiocarps (FIGS. 14, 15) the basidia seem much more uniform in development. The detail of such basidia is shown in figure 37. It is only when the spore-walls are seemingly entirely mature that the nuclei which have been quiescent near or slightly above the center of the basidium move to the upper part of the basidium (FIG. 38). In a number of cases mitosis seemed to occur just as the nucleus entered the basidium, as shown in figure 39 and more highly magnified in figure 440, but very often the nuclei entering the sterigmata appeared as shown in figure 42 and more highly magnified in figure 41. After the passage of the nuclei through the sterigmata two nuclei appear in each spore (FIGS. 43, 44). The basidia soon appear empty and collapse as do the paraphyses also. Figures 18-20 are three magnifications of portions of a large basidiocarp showing these changes. Only rarely can sterigmata be seen. Soon no trace of the hymenial elements, except the spores, remains. A slightly younger, practically mature basidiocarp, such as described in the published paper (1. c.), is shown in figures 16 and 17. The spores have a heavy black wall with a small hyaline apiculus (FIGS. 38, 43-45). Occasionally a spore is observed with a much elongated apiculus as in the lower left portion of figure 20. All basidia are seemingly four-spored.

The description of the development of the basidia given here

differs in many points from that given in the earlier paper (1. c.). A reexamination of the slides made from the original collection upon which that paper was based shows that we had quite adequate justification for the statements made, but that also basidia developing as is here described were undoubtedly present. After seeing stages in the passage of nuclei into the spores and in the spores of actively developing basidiocarps it seems certain that the single nucleus shown in partially matured spores in figure 6 of this paper was not a nucleus but a deeply staining granule, possibly a modification of the granule present at the tip of the sterigma as it developed. Never were nuclei observed in immature spores in the later materials. Many eight-nucleate basidia appeared in the original materials and were occasionally observed in subsequent materials but in all cases there were also evidences of stunted development. It seems probable to the writer that under certain conditions the nuclear division which usually takes place at the base of the sterigma or during the passage of the nucleus through the sterigma might take place earlier and so give rise to eight nuclei in the basidium. In no case could the writer find evidence of the passage of nuclei from such basidia into spores.

In the published paper on Gasterella (1. c.) the occurrence of cystidia in basidiocarps was mentioned. These were present in some and entirely absent in others—a point that was not made entirely clear. No cystidia were ever found in the later materials grown in the laboratory where development seemed to be more vigorous. They were, however, present in basidiocarps of the fungus secured by Mr. Routien during last summer in Michigan as previously mentioned. The fact that they may be present or absent in these fruit-bodies developed under unfavorable conditions lends weight to the idea that they may be modified basidia that during abortion have developed in this manner. Figures 16 and 17 are photographs of one of the very typically small basidiocarps that contain these cystidia.

#### GENERAL CONSIDERATIONS

Since the published paper was based on scanty material and the measurements taken from prepared slides, variations from the original description should be noted. The basidiocarps may attain RO

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a diameter of 1225  $\mu$  or possibly larger. The spores from fully matured dry basidiocarps when mounted in 7 per cent KOH are  $11-16 \times 13-17 \,\mu$  including the apiculus and the verrucose warts on the spores. The apiculus is hyaline and usually about  $2-3 \,\mu$  long in fresh material. In herbarium material of old basidiocarps and especially those that have collapsed and look much like tiny black cup fungi the apiculus can not usually be distinguished. It seemingly becomes brown and appears, if visible at all, as an especially large wart. Cystidia are rarely present and were only observed in depauperate basidiocarps developed in very warm weather. The color of the basidiocarps varied from white when young to ashy gray as they mature and inky black in their final stage. Only four-spored basidia were observed.

The extremes of variation observable in *Gasterella*, if seen in different collections, would readily suggest several species, but since every gradation from tiny basidiocarps with a uniform, unfolded hymenium, with or without cystidia, lining the single locule, except for a restricted sterile region above the point of attachment, up to relatively large fruit-bodies with a much folded hymenium were seen, it seems positive that these are variations within a single species. The extremes of variation observed probably indicate great plasticity such as might be expected in a truly primitive form.

In the earlier paper by S. M. Zeller and the writer (l. c.) Gasterella was tentatively placed in the Protogastrales and Protogastraceae because both are unilocular. It was, however, pointed out that Gasterella differed from Protogaster basically in that Gasterella has a sterile base with a definite point of attachment which is lacking in Protogaster and spores characteristically different in shape and markings and that those of Gasterella suggest a relationship to Hymenogaster. Fischer, in a reclassification of Gasteromycetes, taking into consideration his own researches and those of others, bases his classification upon the origin of glebal chambers in the development of the basidiocarp. Only studies on mature basidiocarps of Protogaster have been possible up to the present. These indicate a locular type of development for Proto-

<sup>&</sup>lt;sup>7</sup> Fischer, Ed. Unterklasse Eubasidii Reihe Gastromyceteae. Engler und Prantl, Die natürlichen Pflanzenfamilien. 2. Auflage, Bd. 7a. 1933.

gaster while the present study shows definitely that in Gasterella the early development is campanulate. With these basic differences it seems impossible to place these genera in the same family. It was also previously pointed out that Rehsteiner 8 in his study of Hymenogaster verrucosus Bucholtz (H. Rehsteineri) found it to be unilocular in its early development but that this condition was soon changed to a multilocular condition by proliferation and the origin of new chambers. The present study shows definitely that in Gasterella its early companulate development is essentially like that of H. verrucosus but in Gasterella development is arrested at this stage so that it permanently has only one glebal chamber even after extensive proliferations of the hymenium have taken place. Thus according to Fischer's interpretation, and especially as discussed in his 1936 paper, Gasterella is clearly related to Hymenogaster. Because of the characteristics pointed out above, it seems possible that Gasterella should be removed from the Protogastrales and placed in the Hymenogastrales as the simplest known genus of the Hymenogastraceae. It may, however, be deemed best to place all simple, unilocular forms together in the Protogastrales, based only on this one characteristic, but in a separate family. This is a problem for the consideration of systematists.

#### ACKNOWLEDGMENT

The writer is indebted to Dr. S. M. Zeller for reading a first draft of this paper and making suggestions.

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#### EXPLANATION OF FIGURES

Photograph Figs. 1–20. Fig. 1 by Richard Hufnagle, otherwise by author. Fig. 1, Gasterella as it appears on soil slightly magnified; 2, 3, origin of locule by differentiation of palisade layer in upper portion  $(2 \times 50, 3 \times 125)$  (See also figs. 21 and 22); 4, slightly older basidiocarp with binucleate basidia  $(\times 125)$ ; 5–7, older basidiocarp with binucleate basidia, 5 and 6, slightly tangential, 7 median  $(5 \times 50, 6 \text{ and } 7 \times 125)$ ; 8, median section of

<sup>8</sup> Rehsteiner, H. Beiträge zur Entwicklungsgeschichte der Fruchkörper einiger Gastromyceten. Bot. Zeit. **50**: 764–771. pl. 10 f. 1–6. 1892.

<sup>9</sup> Fischer, Ed. Neue Beiträge zur Kenntnis der Verwandtschaftsverhältnisse der Gastromyceten. Ber. Schweiz. Bot. Ges. 45: 231-247. 1936.

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basidiocarp with many uninucleate basidia—hymenium conspicuously folded above a sterile basal region ( $\times$  50); 9-10, median section of basidiocarp with 4 nucleate basidia, some showing beginning of sterigmata—basal sterile region nearly obliterated (9  $\times$  50, 10  $\times$  125); 11-13, median (11) and tangential (12) sections of a typical large basidiocarp showing sterile region at base and types of hymenial folding ( $\times$  50)—various stages in the development of sterigmata and spore initials are present (See fig. 36). 13 shows the lower left-hand portion of fig. 11 ( $\times$  125); 14, 15, median section of a common type of basidiocarp: the walls of the spores are approaching maturity (14  $\times$  50, 15  $\times$  125); 16, 17, median section of a mature small basidiocarp of the type developed during very hot weather showing lack of folding of hymenium, sterile basal region, and an occasional cystidium in the hymenium (16  $\times$  50, 17  $\times$  125); 18-20, parts of a mature large basidiocarp: 19, part of median section ( $\times$  50); 18 and 20 portion of hymenium (18,  $\times$  125 and 20,  $\times$  200).

Figs. 21-45. Drawing made by aid of camera lucida with Zeiss lenses. Scale as indicated at lower left except figs. 21, 22, 40, 41, where indicated below drawing. Fig. 21, slightly diagrammatic drawing of the very young basidiocarp shown in figs. 2 and 3; 22, detail of palisade layer seen in fig. 21; 23, slightly diagrammatic drawing of a little older basidiocarp; 24, detail of hymenium shown in fig. 23; 25, portion of hymenium with very young uninucleate basidia; 26, portion of hymenium just before meiosis in basidia (shown on margin of hymenial fold); 27-35, successive stages in basidial development; 33, portion of a basidiocarp just before beginning of sterigmatal development to show detail of all regions; 36, portion of hymenium from basidiocarp shown in fig. 13; 37, basidia with half grown spore walls and paraphyses; 38, basidium showing two of four sterigmata and mature spore walls just before passage of nuclei into spores; 39-40, division of nuclei in base of sterigmata; 41-42, passage of nuclei into sterigmata. Mitosis not seen; 43, end of basidium just after passage of nuclei into spores (spores binucleate); 44, typical mature spore with hyaline apiculus; 45, apical view of spore.

# A THIRD SPECIES OF MASTIGOSPORIUM ON GRAMINEAE <sup>1</sup>

RODERICK SPRAGUE <sup>2</sup>
(WITH 1 FIGURE)

The commonest leaf spot on Dactylis glomerata L. and on Agrostis spp. in Oregon was recently shown to be caused by a fungus that the writer has called *Mastigosporium calvum* (Ellis & Davis) Sprague.<sup>3</sup> According to Articles 16 and 60 of the present International Rules of Botanical Nomenclature (1935), varietal names raised to specific rank are not valid when a specific epithet is available. As pointed out by the writer in the previous article,3 rubricosa of Fusoma rubricosa Dearn. & Barth, is the oldest species name applied to this fungus. Therefore, Mastigosporium rubricosum (Dearn. & Barth.) comb. nov. is the preferred combination. This species, M. rubricosum, which has navicular, hyaline spores (FIG. 1, A) occurs in both North America and Europe, while a second European species, M. album Riess, which has terminal appendages, has not been reported from the western hemisphere. The spore of M. rubricosum illustrated in figure 1, A, was taken from Trisetum cernuum Trin. collected at Bergsvik Creek, Clatsop County, Oregon, March 16, 1939 (O. S. C. No. 417), on which species of grass this fungus had not been previously reported.

A third species of *Mastigosporium* was found on leaves of *Bromus vulgaris* (Hook.) Shear along Mehl Creek, a small tributary of the Umpqua River in Douglas County, Oregon, February 18 and March 7, 1939. The native host, called narrow-flowered

<sup>&</sup>lt;sup>1</sup> Cooperative investigations by the Division of Cereal Crops and Diseases, Bureau of Plant Industry, U. S. Department of Agriculture, and Oregon Agricultural Experiment Station. Published as Technical Paper No. 313 with the approval of the Director of the Oregon Agricultural Experiment Station. Contribution of the Department of Botany.

<sup>&</sup>lt;sup>2</sup> Associate Pathologist, Division of Cereal Corps and Diseases, Bureau of Plant Industry, United States Department of Agriculture.

<sup>&</sup>lt;sup>3</sup> Sprague, R. Two *Mastigosporium* leaf spots on Gramineae. Jour. Agr. Res. 57: 287-299. 1938.

brome, is scattered through moist fir woods at moderate altitudes in the Coast and Cascade mountains of the region. The fungus is probably native.

The fungus produces speckled brown lesions which coalesce to form mottled areas along the sides and terminal halves of the

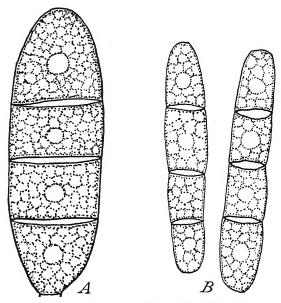


Fig. 1. Conidia of: A, Mastigosporium rubricosum; B, M. cylindricum, × 2000.

leaves. The spores, which are not abundant, are capsular, three-septate, hyaline with large nuclei (Fig. 1, B). They are not only much smaller than those of M. rubricosum but are regularly cylindrical instead of navicular or elliptical. Their manner of developing on stout conidiophores and maturing from the apex down is typical for Mastigosporium, however. The fungus appears to be an undescribed species, for which the following name is proposed:

## Mastigosporium cylindricum Sprague, sp. nov.

Maculis brunneis, ellipticis, dein confluentibus, myceliis hyalinis, endophytis, septatis, conidiophoris hyalinis, brevibus, conidiis hyalinis, sparsis v. subnumerosis, cylindraceis, (capsularibus) tri-septatis,  $25-32 \times 4.5-9 \mu$ . Hab. in foliis vivis *Bromi vulgaris*.

Spots brown, elliptical to elongate, finally confluent and mottled, commonest along the sides and tips of the leaves. Mycelia mostly endophytic, somewhat coalesced beneath the upper leaf surface, coarse, hyaline or lightly tinted, producing short, stout conidiophores which produce the spores by expansion of the distal portion and eventual abscission. Spores straight sided, slightly or scarcely constricted at the septa, cylindrical with rounded, blunt ends, typically capsular, hyaline, 3-septate,  $25-32 \times 4.5-5.9 \mu$ .

On living leaves of *Bromus vulgaris* (Hook.) Shear in fir woods 600 feet above the Umpqua River along Mehl Creek between Elkton and Kellogg, Douglas County, Oregon, Feb. 18 (O. S. C. No. 488, Type, Fig. 1, B) and March 7, 1939 (Nos. O. S. C. 482–487). Specimens have been deposited in the herbarium of Oregon State College and in Mycological Collections of the Bureau of Plant Industry, U. S. Department of Agriculture.

# CERTAIN NUCLEAR PHENOMENA IN ALBUGO PORTULACAE

RUSSELL B. STEVENS
(WITH 8 FIGURES)

The story of sexual reproduction in Albugo candida as worked out by Wager (6), Davis (2), F. L. Stevens (5), and others is well known, involving as it does the formation of oogonia and appressed antheridia within the host tissue. Development of an oogonium is marked by the accumulation of much of the cytoplasm in the central portion of the enlarged hyphal structure, during which process the first mitosis takes place, followed by the differentiation of the contents into a dense homogeneous ooplasm with its well-developed coenocentrum and a vacuolate periplasm. Whether all nuclei pass from the ooplasm and a single one slips back to remain without division (2), or whether several nuclei remain in the central ooplasm and after a mitosis all but one migrate to the periplasm (5), the end result is the same, namely, a uninucleate oosphere with prominent coenocentrum separated from a vacuolate multinucleate periplasm. At this point a male nucleus derived from the intruding fertilization tube unites with the egg nucleus, and subsequent divisions within the zygote formed give rise to the multinucleate resting oospore.

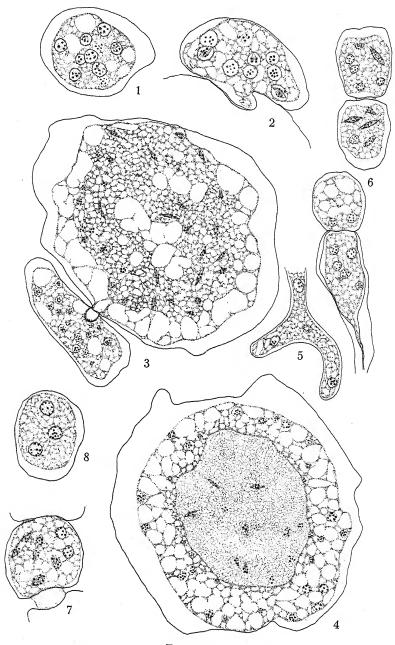
The ontogeny of Albugo Portulacae (DC.) Kuntze resembles in general outlines that of A. Bliti (4), but differs from A. candida in several respects. The process of differentiation in the oogone of A. Bliti involves the crowding of the nuclei, undergoing mitosis, first into an indefinitely outlined zone away from the immediate center, and then to a point outside a sharply formed boundary (5, Figs. 2, 3). As a consequence of the orientation of certain of the spindles at right angles to the boundary of the ooplasm, completion of the mitosis results in the reëntrance of many nuclei into the oosphere. A second mitosis, involving only the nuclei of the oosphere, ensues, all the daughter nuclei remaining within the

ooplasm and functioning as female nuclei. In this species, the receptive papilla seen in A. candida (6) is more highly developed (5, Figs. 1, 5) and forms later, sometimes during the second mitosis. Fertilization in A. Portulaçae is characterized by the fusion of the numerous female nuclei individually with male nuclei resulting from two mitoses in the antheridium simultaneous with those in the oogonium. No division of the fusion nuclei takes place prior to overwintering.

Before the appearance of Stevens' paper (5), Berlese (1) had investigated the formation of sex organs in A. Portulacae and had found several divisions of a smaller number of nuclei in the oogonium, fewer nuclei in the antheridium, no receptive papilla, and at time of fertilization a uninucleate condition of both antheridial tube and oosphere. In fact, these results differed so widely that Stevens in his paper suggests the possibility that they were observing different organisms.

The present observations seem in accord with those of Stevens (5), and figures 3 and 4 of this paper are easily identifiable with figures 2 and 7, respectively, of his report. Indeed, many of the stages described and figured by Stevens were observed, and it is intended to take no significant exception to the general sequence of events as reported.

Stevens reports, and figures (5, Figs. 2, 3), a definite nuclear membrane around each spindle of the first mitosis in the oogonium, and the lack of any such membrane around those of the second. Both of the mitoses within the antheridium have, according to him, spindles surrounded by a nuclear membrane similar to those of the first mitosis in the oogonium. No such nuclear membrane appears about the mitotic figures of the first division in the oogonia (FIG. 3) of the material here examined, but rather there is a close resemblance between such figures and those of the second division (FIG. 4). Nuclei at metaphase stages of the first mitosis in the antheridium (FIG. 2), on the other hand, clearly show a surrounding membrane. On the basis of this, the possibility exists that both oogonial mitoses have spindles which develop after the disappearance of the membrane, but that the membrane persists about the developing spindles of both antheridial mitoses as already described. No trace was seen of the prominent centrosomes noted



Figs. 1-8.

by Stevens (4) in A. Bliti. Further, no structure undeniably a nucleolus was found, though it is not impossible that it was overlooked.

A brief description of the formation of conidia was included in the first description of the genus (as Cystopus) by Léveillé in 1847, and further described for A. candida by Berkeley in 1848, and for A. Portulacae by L. R. Tulasne in 1854. In the present material the formation of the conidia, with one important exception, agrees with the generally accepted story for the genus (3), showing the basipetally developing chains of spores, the coenocytic thick-walled conidiophores, and the gelatinous disjunctors. In addition, definite mitotic figures occur in the conidia, characteristically showing in the second, third, and fourth spores from the base of the chain (FIG. 6). Seldom if ever are all of the nuclei of the multinucleate conidia involved, although the number of dividing nuclei may range from a single one to as many as five or six. By the time a given conidium has become the fifth or sixth from the base, all nuclei are in a resting condition (FIG. 8).

Mitotic figures in maturing conidia closely resemble those in the oogonia, and neither nuclear membrane nor centrosome-like structures are recognizable. The spindle itself is at times somewhat curved, and during anaphase stages (Fig. 7) the fairly uniform spherical chromosomes move at varying speeds to the poles. As the age of a conidium increases, the cytoplasm becomes more finely vacuolate and uniform in structure.

Stevens (4, 5) describes a resting nucleus as showing a prominent nucleolus and a faint "linin" network, with no chromosome-like bodies evident until the prophase stages of an incipient mitosis. In the present material there is a strong suggestion (Fig. 5) of the presence of relatively large chromatin aggregations throughout the resting stage. The nuclei of the vegetative hyphae (Fig. 5), of the young oogonia (Fig. 1), of the antheridia just prior to the first mitosis (Fig. 3), of the periplasm at the time of the second oogonial mitosis (Fig. 4), of the conidiophores (Fig. 6), and of the mature conidia (Fig. 8), as well as those accompanying the dividing nuclei of the young conidia, are similar in structure. These nuclei show several prominent, irregularly arranged, darkly staining bodies with few if any interconnecting strands, enclosed

within a nuclear membrane. These dark granules of the resting nuclei differ little in size from the chromosomes of the mitotic complex, and the number in each case is approximately eight, although the count is rendered somewhat uncertain by the minuteness of the nuclear structures. This evidence strongly suggests that they are prochromosomes.

The material used in this work was collected on *Portulaca ole*racea at Madison, Wisconsin, and was fixed in Carnoy's solution. All of the figures were drawn from slides stained by the iodinegentian violet-picric acid technique, with the exception of figure 2, which was taken from a Heidenhain's haematoxylin preparation.

The writer wishes at this point to express his appreciation to Dr. E. M. Gilbert of the Botany Department for advice and criticism, and particularly to Dr. D. C. Cooper of the Genetics Department for the excellent slides on which the observations were made.

#### SUMMARY

- 1. The mitotic spindles of both first and second divisions in the developing oogonia of A. Portulacae appear to form after the disappearance of the nuclear membrane.
- 2. The spindles of the first antheridial mitosis are surrounded by the nuclear membrane at least as late as the metaphase stages. Spindles of the second mitosis were not observed.
- 3. In neither oogonia nor antheridia were centrosomes or nucleoli recognized.
- 4. Division figures closely resembling those in the oogonia appear in the maturing conidia, usually in the second, third, or fourth spore from the base of the chain. Not all the nuclei in a given spore undergo division, and older conidia show only resting nuclei.
- 5. Resting nuclei, wherever found, show dark granules which resemble in size and number (approximately eight) the chromosomes of the mitotic figures, and which are in all probability prochromosomes.

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MADISON

#### LITERATURE CITED

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#### EXPLANATION OF FIGURES

Fig. 1, young oogonium, showing nuclei in resting condition ( $\times$  1115); 2, antheridium, in first mitotic division, showing intranuclear spindles ( $\times$  1675); 3, oogonium in early stages of zonation, showing numerous nuclei in metaphase of first mitosis, devoid of nuclear membrane or centrosomes ( $\times$  1115); 4, oogonium, fully differentiated into ooplasm and periplasm, with nuclei of ooplasm in metaphase of second mitosis and periplasmic nuclei in resting condition ( $\times$  1115); 5, portion of vegetative hypha ( $\times$  1115); 6, conidiophore and four basal conidia, showing nuclear divisions in the conidia and resting nuclei in the conidiophore ( $\times$  1675); 7, conidium showing divisions in anaphase stages, and chromosomes moving at varying speeds to poles ( $\times$  1675); 8, mature conidium with all nuclei again in a resting condition ( $\times$  1115).

## STUDIES IN THE GENUS TYPHULA 1

RUTH E. REMSBERG (WITH 58 FIGURES)

The literature on the genus *Typhula* records at least eighty species. A few are frequently collected and are well described; many more are rarely collected and consequently only meager and unsatisfactory descriptions are available. It is evident that all recorded names do not represent distinct species. The student in mycology soon becomes bewildered with the current taxonomic situation in this genus, and is usually discouraged in his study of the group. It was with this situation in mind that this investigation was undertaken, and a study of these fungi has brought to light many interesting facts.

#### HISTORICAL ACCOUNT OF THE GENUS

Persoon (25) first recognized Typhula as a distinct group of fungi and made it a sub-division of Clavaria, using the subcapitate character of the clavula as a basis of separation from the other species of Clavaria. Fries elevated this sub-division to generic rank (10), retaining the name Typhula, and stating that the group composes a natural genus by virtue of cylindrical, fertile clavulae and distinct, filiform stipes. He lists four species: T. erythropus, T. gyrans, and T. phacorrhiza as having sclerotia present, and T. Todei with the sclerotium absent. The genus Typhula was retained by Fries in his Systema Mycologicum under the sub-order

<sup>1</sup> Also presented to the faculty of the Graduate School of Cornell University, June 1938, as a major thesis in partial fulfillment of the requirements for the degree of doctor of philosophy.

The writer wishes to express her sincere appreciation to Prof. H. H. Whetzel, under whom this investigation has been made, whose advice, suggestions, and criticisms during the study and in the preparation of this manuscript have been extremely valuable. Special acknowledgment is also due Dr. F. J. Seaver, N. Y. Botanical Garden, and Miss Anna Jenkins, Bureau of Plant Industry, for their assistance in making available many descriptions of species of fungi.

Clavati of the Hymenomycetes. He again separates it from the other genera by its slender, fertile clavula and distinct, filiform, sterile stipe. Eight species are listed: T. gyrans, T. phacorrhiza, T. erythropus, T. villosa, and T. ramentacea with sclerotia present, and T. Todei, T. tenuis, and T. filiformis in which the sclerotia are said to be absent. The characteristic upon which he divides the genus into two groups is the presence or presumed absence of sclerotia. Persoon (26), however, does not recognize the generic rank which Fries gave Typhula in his Observationes Mycologicae and in his Systema Mycologicum. The genus was still maintained by Fries in his Epicrisis Systematis Mycologici, and it has retained this rank throughout mycological literature to the present time.

Although the basidiomycetous nature of *Typhula* was not determined until after the middle of the nineteenth century, Fries stated that the spores in the closely related genus *Pistillaria* are emergent (11). Previous to that time, and for many years afterward, the spores were apparently not observed, or else the fruiting hymenium of these fungi was mistaken for an ascigerous layer. Berkeley (3) called attention to the fact that members of the Clavariei belong to the group of fungi in which the spores are borne exogenously on filiform apicules arising from an enlarged cell. Fuckel (14) was apparently the first to place the genus *Typhula* under the Basidiomycetes.

In Fries' last large taxonomic work on the group, Hymenomycetes Europaei, there are listed 23 species. Twelve have sclerotia and are brought together under the sub-division *Phacorrhiza*. Under *Leptorrhiza* he places those species which are said to be without sclerotia. These two divisions *Phacorrhiza* and *Leptorrhiza* are retained in almost all subsequent taxonomic treatments.

Much of the confusion in the taxonomy of these fungi arises from the attempt to separate species of *Typhula* from the closely related forms usually referred to *Pistillaria*. The genus *Pistillaria* was established by Fries (11) to include those fungi with slender fruit-bodies resembling those of the Typhulae, but in which a distinct stipe is lacking and with the hymenium covering the entire surface. Fries felt that this separation is unsatisfactory, and it has been found since that there are many overlapping forms in the two genera.

The genus *Pistillaria* gradually came to cover those forms which have, for the most part, two-spored basidia and no distinct stipe. Winter (38) and Schroeter (32) both follow this line of separation. Winter notes that in both genera, as at present constituted, are to be found forms with or without sclerotia, and that it is probable that sclerotia have not yet been found for some species of *Typhula*. This same separation of the species into two genera is given by Hennings (16) and Killerman (19); the two-spored forms without sclerotia being placed in *Pistillaria* and the four-spored forms with sclerotia in *Typhula*.

In the more recent taxonomic treatments by Saccardo (30) and Bourdot & Galzin (5), *Pistillaria* is treated to include forms with one to four spores, and *Typhula* forms with two to four spores. In both these works keys are given to a large number of species, based chiefly on sporophore characteristics.

Coker (8) does not use either the number of spores on the basidium or the presence or absence of sclerotia to separate Typhula from Pistillaria. He uses the character of the stipe as the chief basis for referring species to the respective genera. Those with short stout stipes he places in the genus Pistillaria; those with distinct, long filiform stipes in the genus Typhula. Coker also points out that there is some confusion as to the generic identity of certain small species which on account of the absence of sclerotia he refers to Clavaria. Previous workers distinguished the two groups on the basis of the slender filiform cartilaginous consistency of Typhula species in contrast with the larger stouter, fleshy consistency of those of Clavaria. However, Coker indicates that some species of Clavaria are to be excluded from Typhula solely by virtue of their size and indistinct stipe. He apparently attributes little significance to the presence or absence of sclerotia.

From a review of the taxonomic literature, it is evident that no entirely satisfactory basis for separating *Typhula* from related genera, and especially from *Pistillaria* has been proposed. The cartilaginous consistency and small size of the sporophores, with the fertile hymenium limited to a clavula usually serve to distinguish them from *Clavaria*. However, under the present systems, there are some border line species which are difficult to place. The use of the number of spores on a basidium as a character in dis-

tinguishing species of *Typhula* and *Pistillaria* is untenable, since two-spored and four-spored basidia are to be found in typical species of both genera. The presence of sclerotia appears to the writer to be the most reliable single character for distinguishing species of *Typhula* from those of *Pistillaria* or *Clavaria*. The presence of a swollen hymenial portion, the clavula, distinct from the filiform stipe, also appears to be a characteristic of *Typhula* species.

#### METHODS AND RESULTS OF INVESTIGATIONS

A great deal of interest has been aroused during the past fifteen years concerning the injury caused by pathogenic species of Typhula in cereals and grasses. Serious injury to winter wheat was first reported in the United States in 1922 from Fremont and Teton Counties in Idaho (17). At that time the disease was attributed to Sclerotium rhizodes, but examination of material collected then has shown it to be a species of Typhula. It has occurred nearly every year since in various northern and high altitude wheat sections of that state. It has also been reported from Washington (15) and Montana (40, 39), as well as from Japan (4, 20, 18, 33) and Germany (9, 21, 23, 36). The disease is most commonly found in localities where the snow remains on the fields late in the spring. Accounts of investigations of the disease in the Western United States is given by Remsberg and Hungerford (29) and by Young (41). The same species of Typhula has been collected on lawn and turf grasses in Idaho, New York, and Pennsylvania. Many other species are collected frequently on overwintered herbaceous stems and leaves, where they have probably developed saprogenically.

Sclerotia are as a rule to be found in great abundance, but very rarely have the sporophores been observed. Since all previous taxonomic treatments are based chiefly on sporophore characters, it was found very difficult to identify our collections of sclerotia with the described species. These fungi are readily grown on agar where large numbers of sclerotia are easily produced, but seldom had fertile sporophores been obtained in culture. The problem then became one of determining under what conditions these fungi fruit and to duplicate these conditions experimentally.

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It soon became apparent from field observations and from studies of the fungi in culture that many of the species, especially the pathogenic ones had unusually low optimum temperatures. In culture these optimum temperatures range from 6–12° C., with abundant growth as low as 0–3° C. In the field the pathogenic species are found growing just under the edge and beyond the receding snow. The saprogenic species are also usually found in greatest abundance just after the snow has melted. When the fruiting bodies of *Typhula* have been collected, it is usually during the rainy cold weather of autumn, or in the case of some species, in the early spring. Hence, it appeared that optimum conditions for fruiting are cold weather, abundant moisture, and high humidity.

Numerous attempts were made to produce sporophores in culture on agar by varying the nutrients, temperature, and light in the laboratory, but in all cases sterile sporophores only were produced. Other experiments were performed in which the sclerotia, produced either in culture or collected in nature, when placed on sand at low temperatures always resulted in the production of sterile sporophores. In order to obtain fluctuating natural temperatures, sclerotia were placed out-of-doors in glass containers, but always failed to produce fruit-bodies. Since in all these experiments the sclerotia were either under glass or in total darkness, it became evident that another condition necessary for fructification might be direct daylight. Tasugi performed similar experiments in Japan with the same results, but found that sclerotia gave normal fruiting when exposed directly to natural daylight (33) or under vitaglass (34).

With these factors in mind, the following experiment was set up. A wooden cigar box supported by a block of wood at each corner was placed in a shallow aluminum pan. First, a layer of peat or sphagnum moss was placed in the box and then a layer of sand was put in on top so that the box was approximately half full. Water was kept in the bottom of the pan and cheese cloth was placed over the box in such a manner that it hung down over the sides and into the water in the pan. In this way the cheese cloth acted as a wick to draw the water up over the box, thus keeping the sand moist and maintaining a high humidity.

An abundant supply of sclerotia was obtained by growing the fungi in culture on potato dextrose agar or on sterilized wheat kernels. These sclerotia were placed on the surface of the sand, and the pans and boxes were put out-of-doors in diffused daylight during the months of February, March, and April, 1936 and 1937. During the time when the outdoor temperature remained near 0° C. for most of the day and night, and cold rain and snow flurries prevailed, numerous sporophores developed. These appeared in two to four weeks after planting the sclerotia, depending on the species and the weather conditions. These experiments were repeated in the autumn during September, October, and November, with the same results during those years.

These experiences suggested that short rays of natural daylight, which are not transmitted through ordinary glass, play an important role in the stimulation of the fungi to fructification. An abundance of sporophores were then obtained under artificially controlled conditions which closely approximated the natural conditions under which they had previously appeared. The pans and boxes were placed in a refrigerator room in which the temperature was kept at 32–38° F. A source of ultra-violet light was provided by employing a General Electric Sunlamp, Model F, using an Edison S-1 sunlamp bulb. This was installed in such a manner that the boxes were 20–30 inches from the source of light. An exposure for a total of two hours daily was given. In 2–4 weeks, typical sporophores developed. It was thus possible to duplicate artificially the optimum natural conditions for fructification and to obtain sporophores at will during any time of the year.

In order to determine the character of the light waves which seemed to be influential in the stimulation of fructification, a series of filters was used in an experiment set up out-of-doors as described above. The filters were placed over the boxes under the cheese cloth. Where ordinary window glass was used, no sporophores were produced. It has been shown that common window glass does not transmit light of shorter wave length in the ultra-violet region of the spectrum than approximately 3250 Angstrom units.<sup>2</sup> However, when vitaglass,<sup>3</sup> which transmits light waves of 2650-

<sup>&</sup>lt;sup>2</sup> Pamphlet: Glass color filters manufactured by Corning Glass Works, Corning, New York, 1935.

<sup>&</sup>lt;sup>3</sup> Supplied by the Vita Glass Corporation, New York City.

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6690 Angstrom units, was used as a filter, normal fruiting of the fungi took place. The range of light which stimulates fructification is thus indicated to lie between 2650 and 3250 Angstrom units. Fertile sporophores are produced under the Corning glass filter No. 970 Corex D.<sup>4</sup> This glass transmits at least 60 per cent in the region of 3020 Angstrom units, with a sharp decrease to 10 per cent at 2700 Angstrom units. It is indicated by these experiments with the filters that the region which apparently stimulates fructification of *Typhula* lies approximately in the region between 2700 and 3250 Angstrom units.

## CULTURAL STUDIES

These fungi are easily obtained in culture on potato dextrose agar from sclerotia, diseased tissue, or from shot basidiospores. The sclerotia or pieces of diseased tissues were surface disinfested with calcium hypochlorite 5 and planted directly on the agar. Sporophores were fastened inside on the lid of a petri dish and the basidiospores were allowed to shoot down onto the surface of the agar.

The temperature range for growth was determined for each species studied. All fourteen species made fairly good growth at 0° C. Growth at temperatures below 0° was not tested. The maximum for all the species varied between 18° and 27° C. The optimum for three of the species was relatively low, being in the neighborhood of 6–12° C. The optimum for the other species lay between 12° and 21° C. The minimum, maximum, and optimum temperatures for growth for each species will be found in the notes under taxonomic studies.

It will be found that the range and optimum temperatures for the pathogenic species run consistently low as compared with the saprogenic species. This is in direct correlation with the fact that the pathogenic activities of *T. Itoana*, *T. idahoensis*, and *T. um*brina occur at low temperatures in the field and garden.

Mycelial growth on potato dextrose agar in most species is typi-

<sup>4</sup> Supplied by the Corning Glass Works, Corning, New York.

<sup>&</sup>lt;sup>5</sup> A fresh solution of 10 g. calcium hypochlorite in 140 cc. water was used according to the formula given by Wilson (37). The material to be disinfested was allowed to remain in the solution 5-15 min.

cally of a radiating fan-shape, and may or may not be accompanied by fluffy aerial mycelium. In other species it may consist of an extremely suppressed or submerged mycelial growth of hydrotic aspect. In the majority of the species a brown stromatic crust is formed at or near the maximum temperature for growth (FIG. 5). This crust is of the same nature as the sclerotial rind, the hyphae becoming gnarled, enlarged, thickened, and agglutinated into a more or less compact hardened layer. In the case of *T. gyrans* and *T. phacorrhiza* the mycelial growth in the agar becomes a tough cartilaginous layer difficult to cut or break.

Sclerotia appear in culture in 5 days to 2 weeks and are formed singly (FIG. 2), in coalesced masses (FIG. 3) or in concentric rings (FIG. 4). At extreme low temperatures there is a tendency for the sclerotia to grow in piles or masses, while at extreme high temperatures they are scattered. In all cases there is an abundant extrusion of moisture from the sclerotia during formation. When drops of this liquid are dried on a glass slide, a crystalline residue or deposit is formed.

In many species there is a tendency toward formation of a-typical, sterile sporophores in culture (FIG. 6). These may develop from sclerotia, stromatic cursts, or from mycelial mats on the surface of the agar. In some instances these may approach the appearance of typical sporophores, but usually remain sterile. However, *T. sphaeroidea* has been observed to form fertile sporophores from mycelium on agar in culture on rare occasions at 9–21° C. These sporophores resemble very closely those produced under natural conditions.

#### GENETIC MORPHOLOGY

A critical study of the morphology of the species at our disposal was made in the hope of finding characteristics which would serve in the identification of species and to disclose, if possible, a more satisfactory basis for defining the generic concept for this group of forms.

A study of the development of the sclerotium agrees with the account given by DeBary (1). A tuft of much branched hyphae arises from the mycelium in the substratum, and becomes a ball of enlarged hyphal cells. It increases in size by repeated branching

of the hyphae as they become intertwined. The peripheral cells become fused early, and consequently are much distorted as the sclerotium increases in size. These peripheral cells become the thickened gelatinized rind, and the intertwining hyphae within become the medulla, which is rich in stored food material. When these balls of hyphae develop in isolated positions, the sclerotia are formed singly; when the sclerotial initials arise close together, they often fuse with each other so that when the rind develops, it will enclose several balls, thus giving rise to coalesced sclerotia.

Very little mention is made of sclerotial morphology in any of the taxonomic treatments, other than meager descriptions of the general shape, size, and color. However, DeBary (1) discusses two types of medulla construction found in species of Typhula. He observed in T. variabilis that the medulla is made up of enlarged intertwined hyphae with here and there inter-hyphal spaces, while in T. phacorrhiza the medulla is of cartilaginous consistency in which the gelatinous cell walls have completely fused so that the lumina of the cells appear to be embedded in a continuous hyaline matrix. Both these types have been found to exist in the species studied. The medulla first described may be said to be of a prosoplectenchymatous 6 type (FIG. 38). The second is to be designated as paraplectenchymatous (FIG. 46). In some species, the contacting walls may still be visible, but with no inter-hyphal spaces, appearing to form a solid parenchyma. This third kind of medullary structure may be designated the pseudoparenchymatous type (FIG. 40). Young sclerotia in section may show transition stages in the formation of either of the three types of medulla. In the center will be found small thin-walled, smooth hyphae, others with walls becoming gelatinized and thickened with the lumina appearing crooked. The hyphae become more compact toward the periphery of the sclerotium, and in the case of the paraplectenchymatous medulla, different stages of hyphal fusion will be seen with complete fusion adjacent to the rind. Thus it is seen that in all cases the hyphae of the medulla have thickened gelatinous walls and are not thin-walled as deBary seems to imply (1:35).

The dark colored rind of the sclerotium is either a homogeneous <sup>6</sup> Snell, W. H. Three thousand mycological terms, p. 1-151. 1936.

gelatinous deposit on the outer walls of peripheral hyphal cells (FIG. 46), or is made up of layers of hyphae wound about the medulla (FIG. 45). The walls of these hyphae become thickened and darkened. The hyphae are agglutinated but often sluff away from the surface as the sclerotium enlarges, until but a layer or two is left. The rind cells of all species are enlarged and distorted, so that in surface view they appear in an irregular or angular pattern (FIGS. 32, 33). In some species these cells become tuberculate, often forming miniature rosettes scattered over the surface of the sclerotium (FIG. 37).

The sporophores usually arise directly from sclerotia both in nature and under artificial conditions. They have, however, been observed to arise from the stromatic crusts formed on culture media at high temperatures, and occasionally also direct from creeping rhizomorphic strands or even from mycelial mats. The stolon-like rhizomorphic strands, although originating from the sclerotia placed on sand, often grow along the surface or through debris for some distance before giving rise to the sporophores. Since in collecting the sporophores they are easily detached from the sclerotia and as they do not always arise directly from the sclerotia, it is easy to understand why many collections have been made of the fruit-bodies in which sclerotia apparently have been absent. For this reason, culturing of species suspected of belonging to *Typhula* is of great value in determining whether or not sclerotia are actually produced.

The sporophores are typically small, slender, filiform, clavate bodies of cartilaginous consistency which become hairlike and flexuous when dry, and which will revive to their original size and texture on soaking in water. The sporophore is divided into a distinct, filiform, sterile stipe and a cylindrical clavula bearing the fertile hymenium; it may be completely white or variously colored, according to the species. The sporophore is made up of upright agglutinated, parallel strands of hyphae which give rise to the basidia at right angles in the clavula. These strands of hyphae may be completely fused to give a pseudoparenchymatous aspect to the subhymenium (FIG. 48), or they may be loosely interwoven (FIG. 52).

The basidiospores are produced on slender, hair-like, attenuated

sterigmata at the apex of the basidium. The number of spores to the basidium varies with the different species from two to four, and even six to eight in one species (FIG. 1, b–e). Under some conditions, especially when fruiting sporophores are kept in total darkness for 24 hours, basidia are found producing but one basidiospore, or maturing one at the expense of the others (FIG. 1, a). Since this is of unusual occurrence and is found only under abnormal conditions, it is not considered of any taxonomic importance. The spores of all species studied are of the same general shape, ovate or elongate, inaequilateral, flattened or incurved along one side above the apiculus (FIGS. 53–57) are shot away at maturity and germinate by one or more germ tubes.

It was observed from time to time during these studies that several species of Typhula produced minute micro-conidial-like bodies in abundance in old cultures on potato dextrose agar. These bodies are rod-shaped, cylindrical, approximately  $2\mu$  wide and varying from 4 to  $6\mu$  in length. They are borne on the old mycelium from short lateral branches (Fig. 58). Brefeld illustrates similar bodies for T. variabilis (6: 219, pl. 8, f. 2). The function of these micro-conidia has not been demonstrated.

#### TAXONOMIC STUDIES

The following suggestions for placing the genus *Typhula* more satisfactorily in the taxonomic system are presented as a result of these studies. It seems desirable to place most emphasis on the sclerotia, since they are more frequently and abundantly collected, rather than on the sporophores which are, when found, not strikingly distinct from the sporophores of certain species in related genera.

It is suggested that the genus *Typhula* be used to include those species with small, filiform, clavate sporophores which normally arise from sclerotia, and the genus *Pistillaria* to include similar forms in which sclerotia are wanting. It will often be necessary to grow these fungi in culture to be sure that sclerotia are present or absent in the life cycle. However, since this is a very easy process and one which is of value in determining the morphology of sclerotia for the separation of different species, it is entirely desirable.

If further studies disclose a strict correlation of the slender stipe

and distinct clavula with the presence of sclerotia in *Typhula* and the indistinct clavula and absence of sclerotia in *Pistillaria*, the distinction between the two genera will be strengthened considerably. If this correlation cannot be established, the separation of the two

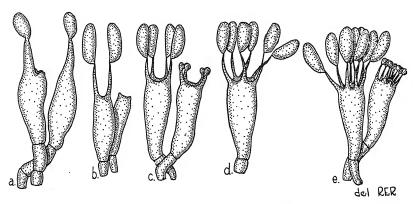


Fig. 1. Basidia and basidiospores of species of Typhula. Approx.  $\times$  450. a, basidia of fruiting sporophores which had been kept in the dark 24 hours, producing but one basidiospore; b, two-spored basidium; c, four-spored basidium; d, six-spored basidium; c, eight-spored basidium.

genera on the basis of the presence or absence of sclerotia alone, still affords a satisfactory and reliable distinction between them.

In this investigation it was possible by culturing the fungi to obtain an abundance of material of both sclerotia and sporophores, so that repeated studies of the species could be made. In this way it was possible to observe variations within a given species which hitherto had lead early workers to erect different species based upon meager or isolated collections. Thus we have been able to reduce to synonymy names of several species found in the literature and disclose many as yet undescribed species.

The characters which have been used here in the separation of species within the genus are chiefly those of sclerotial morphology, although sporophore characters have been drawn upon as far as they are available. Sclerotia produced in culture are found to agree in morphology and color with those obtained in the original collections. Colors are given according to Ridgway.<sup>7</sup>

 $<sup>^7</sup>$  Ridgway, Robert. Color standards and color nomenclature, p. I–III + 1–43. 1912.

TYPHULA Fries, Obs. Myc. 296. 1818. Syst. Myc. 1: 494. 1821

Sclerotia arising from branched, septate, mycelium with clamp connections and frequent anastomoses; white or pale and translucent when young, becoming tawny, reddish-brown, dark-brown or nearly black as the rind develops with maturity; superficial, erumpent or immersed in substrate, adherent or falling away easily, attachment sometimes by minute stalk; single, clustered, or coalesced into masses; smooth, roughened, furrowed or tuberculate, shrunken with age, collapsed after fructification; spherical, subglobose, flattened or concave below, rounded above, or pyriform and flattened laterally; rind colored, composed either of a tough, gelatinous layer deposited on the outer walls of enlarged, peripheral. hyphal cells, or of compactly intertwined hyphae wound about the medulla at the periphery; medulla white or light colored, often cartilaginous, made up of intertwining enlarged, septate, branched hyphae whose lumina become narrow and crooked, and whose walls become thickened, gelatinized and translucent, appearing prosoplectenchymatous, paraplectenchymatous, or pseudoparenchymatous, often containing embedded crystals; solid, with center often composed of loosely interwoven hyphae, or hollow in the case of large sclerotia or coalesced sclerotial masses.

Sporophores cartilaginous, one or more arising from the medulla of the sclerotium, from a stromatic crust, mycelial mat, or creeping stolons which originate from sclerotia; small, clavate, awl-shaped or filiform, erect, straight or curved, flexuous or prostrate, apex acute or obtuse, base filiform; simple or with branches arising at any point along the main axis; translucent when young, opaque when

old or dry.

Clavula straight or curved, cylindrical, flattened or furrowed; composing the upper half or two-thirds of the sporophore; tip sometimes sterile; translucent when young, becoming opaque and pruinose with spores at maturity; often proliferating to form new clavulae; simple or branched with apex attenuate or blunt, and usually sharply distinguished from the stipe; smooth or often pubescent with age; hollow or solid, the subhymenial layer pseudoparenchymatous or loosely interwoven, with or without embedded crystals.

Stipe distinct in size or color from clavula especially at maturity; erect, flexuous, prostrate or creeping, cylindrical, filiform; translucent when young, shiny or dull when dry or old; smooth or pubescent with basal hairs often clasping the sclerotium; solid or hollow, made up of compactly agglutinated, parallel hyphae with or without incrustations.

Basidia 2- 4- 6- or 8-spored, clavate, slender and elongate or

broad and short, hyaline; the a-paraphasate hymenium often obscured by incrustations; adherent or breaking away from subhymenial layer; with or without clamp connections at base.

Sterigmata hyaline, straight and awl-shaped, curved or hooked, tapering to a hair-like tip; about  $8 \mu$  long and  $2 \mu$  wide at the base.

Basidiospores hyaline, smooth, inaequilateral, usually flattened or slightly incurved on one side above an apiculus.

Conidio known.8

Micro-conidia sometimes present in culture, hyaline, smooth, cylindrical, approximately 2  $\mu$  wide and 4–6  $\mu$  in length, borne on short lateral branches from the main hypha, non-germinating (?), function undetermined.

#### TYPE SPECIES

The species Typhula phacorrhiza Reichard ex Fries has been chosen as the neo-type species of the genus Typhula. The first name applied to the perfect stage of any species of fungus later to be placed in Typhula was phacorrhiza, when Reichard (28) used it for a species which he referred to Clavaria. The species Clavaria phacorrhiza was acknowledged by Persoon in his Commentatio de Fungus Clavaeformibus and also in his Synopsis Methodica Fungorum. It is the oldest of the three species of Clavaria elevated by Fries (10) to generic rank under the name Typhula, and was one of the eight species in this genus described in Fries' Systema Mycologicum.

This species has been most frequently collected, is very abundant, and there are more complete descriptions and illustrations in the literature for it than for any other species of the genus. For these reasons it has been chosen as the species typical of the genus.

#### KEY TO SPECIES 9

- Sclerotia with medulla paraplectenchymatous or pseudoparenchymatous, center often somewhat prosoplectenchymatous; rind either a homogeneous gelatinous layer or composed of intertwining hyphae.
- <sup>8</sup> Condia have been frequently observed by the writer both in culture and in nature for a single, as yet unidentified species of *Typhula*. They are produced in great abundance on sporodochia which develop from massed sclerotia or stromata, are large, cylindrical, borne on long conidiophores and germinate by one or more germ tubes.
- <sup>9</sup> The key and following descriptions of species are based primarily on characters exhibited by these fungi grown under artificial conditions, corresponding in general with the characters under natural conditions in so far as we have been able to observe them.

A. Medulla paraplectenchymatous.

- 1. Rind a homogeneous gelatinous layer; sporophores colored.
  - a. Sclerotia superficial, adherent by minute reddish brown stalk, pyriform or flattened laterally on two sides, 1-3 × 4-5 mm., cinnamon-brown to Mars-brown; 10 sporophore filiform, tawny to russet, 20-100 mm. tall. 1. T. phacorrhiza.
  - b. Sclerotia immersed-erumpent, spherical to subglobose, 0.5-4.0 mm., tawny to hazel-brown; sporophore clavate, rose colored, 8-25 mm. tall. . . . . . . . . . 2. T. Itoana.
- Rind composed of intertwining hyphae; sporophores white, often with reddish-brown base.
  - a. Rind <sup>11</sup> cells paraplectenchymatous, extending irregularly into the medulla; medulla paraplectenchymatous throughout or with center of loosely interwoven hyphae bounded by dark cells resembling an internal rind, 0.5-1.0 mm., woodbrown to nearly black; sporophore broadly clavate, 1-3 mm. tall. . . . . . . . . . . . . . . . 3. T. sphaeroidea.
  - b. Rind cells prosoplectenchymatous, in a uniform layer about the medulla; medulla paraplectenchymatous throughout or prosoplectenchymatous in center with no internal rind, 0.5-3.0 mm., natal brown to clove brown; medulla paraplectenchymatous; sporophores 5-15 mm. tall.

4. T. gyrans.

- B. Medulla pseudoparenchymatous.
  - Rind composed of intertwining hyphae; sporophores white with reddish brown base.
    - a. Sclerotia single or clustered, rarely coalesced 0.5-1.0 mm., auburn to chestnut-brown; medulla pseudoparenchymatous; sporophores 2-6 mm. tall. . . . . . . 5. T. Viburni.
- II. Sclerotia with medulla entirely or for the most part prosoplectenchymatous; rind a homogeneous gelatinous layer.
  - A. Medulla immediately adjacent to rind composed of greatly enlarged cells; center prosoplectenchymatous.
    - Sclerotia always single, never coalesced, van dyke-brown to chestnut-brown; sporophores avellaneous to wood-brown, 8–15 mm. tall. . . . . . . . . . . . . . . . . . 6. T. umbrina.
    - 2. Sclerotia single or coalesced; sporophores white or colored.
      - a. Sclerotia large, 3-6 mm., chestnut-brown to nearly black;
         sporophores olive-buff to smoke-grey, 30-50 mm. tall.
         7. T. variabilis.
      - b. Sclerotia small, 0.5-3.0 mm.; sporophores entirely white.

        - 2'. Sclerotia 2-3 mm., bister to nearly black; sporophores 6-22 mm. tall. . . . . . . . . . 9. T. pertenuis.
- $^{10}$  Ridgway, R. Color standards and color nomenclature, p. I–III  $\pm$  1–43. 1912.
- <sup>11</sup> Sclerotia rarely developing on potato dextrose agar. Sporophore here usually arising directly from the mycelium.

- B. Medulla prosoplectenchymatous throughout; cells not prominently enlarged adjacent to rind.
  - 1. Sclerotia always single, never coalesced.
  - 2. Sclerotia single or coalesced.

    - Sclerotia small, 1.5-3.0 mm.; sporophores white or colored, simple.

      - Sclerotia 2.0-2.8 mm.; sporophores light drab to drab, clavula broadened and awl-shape, 9-18 mm. tall.

14. T. subulata.

- 1. Typhula phacorrhiza Reichard ex Fries, Syst. Myc. 1: 495. 1821.
  - Clavaria phacorrhiza Reichard, Schrift. Berl. Ges. Nat. Fr. 1: 315. pl. 1, f. 4, 5. 1780.
  - Clavaria cylindrica Tode, Schrift. Berl. Ges. Nat. Fr. 4: 166. 1783.
  - Sclerotium complanatum Tode, Fungi Meckl. 1: 5-6. pl. 1, f. 9a-d. 1790.

Clavaria hirta Vahl, Pl. Dan. 21: 8. pl. 1257. 1799.

Clavaria triuncialis Pers. Syn. Fung. 1: 600. 1801.

Sclerotium scutellatum Alb. & Schw. Consp. Fung. 289. 1805.

Clavaria triuncialis var. juncea Alb. & Schw. Consp. Fung. 289. 1805.

Clavaria juncea Fries, Obs. Myc. 2: 291. 1818.

Clavaria juncea var. vivipara Fries, Syst. Myc. 1: 479. 1821.

Clavaria virgultorum Pers. Myc. Eur. 1: 186. 1822.

Phacorrhiza filiformis Grev. Fl. Edin. 415. 1824.

Typhula erythropus Schnizlein, in Sturm, Deuts. Fl. Pilze 31: 23. pl. 12. 1851.

<sup>12</sup> This combination and citation is referred to by Winter (38).

Typhula juncea (Fries) Karsten, Hattsv. 2: 181. 1882.

Typhula complanata (Tode) DeBary, Vergl. Morph. Pilze 44. 1884.

Clavaria scutellata DeBary, Vergl. Morph. Pilze 44. 1884.

Typhula subphacorrhiza Britz. Hymen. Südb. 8: 15. f. 77–78. 1891.

ILLUSTRATIONS (in addition to the above): DeBary, Vergl. Morph. Pilze, f. 15a-b, 1884; Berk. Intell. Obs. 1: 289-294. f. 1-2. 1862; Bischoff, Krypt. f. 3397. 1860; Boud. Ic. Myc. 1: pl. 176. 1904; Britz. Hymen. Südb. 8: f. 77-78. 1891; Britz. Bot. Centr. 26: pl. 746. 1910; Bull. Hist. Champ. Fr. 1: pl. 462, f. 2. 1791; Coker, Clavarias, pl. 84, f. 4. 1923; Corda, Ic. Fung. 3: pl. 3, f. 56. 1839; Grev. Scott. Crypt. Fl. 3: pl. 144, f. 1. 1825; Harper, Mycologia 10: 53-57. pl. 5. 1918; Henn. in E. & P. Nat. Pfl. 1: f. 71L. 1900: Herter, Krypt.-Fl. Mark Brandenburg 6: 147, f. 2a-b. 1910; Loudon, Encyclop. f. 16192, 1855; Micheli, Nov. Pl. Gen. pl. 87, f. 7. 1729; Nees, Syst. Pilze Schw. pl. 14, f. 139-140. 1816; Pat. Tab. Anal. Fung. 3: pl. 469. 1883; Sicard, Hist. Nat. Champ. f. 326. 1884; Smith, Syn. Br. Basid. f. 110A. 1908; Stevenson, Hymen. Brit. 2: f. 94. 1886; Winter, in Rab. Krypt.-Fl. 1: 293. 1884.

Material examined: C. U., 13 Rab. Fungi Eu. 239 Typhula phacorrhiza Fries; Krieger, Fungi Sax. 417 and 418 Typhula complanata DeBary; Krieger, Fungi Sax. 1421 Typhula juncea Alb. & Schw.

Sclerotia (Fig. 10) tawny to russet, later cinnamon-brown to Mars-brown, superficial on substrate, very adherent by minute dark-brown or reddish-brown stalks, single or massed into clusters, lobed and irregular in shape, smooth at first, becoming wrinkled or furrowed on drying or with age, very cartilaginous in consistency, pyriform with stalk at narrowed end, apex often broadened, rounded or lobed, characteristically flattened especially on drying or aging, when single, 1–3 by 2–4 by 3–5 mm. in size, when coalesced, the masses are 10–15 mm. in diameter; rind (Fig. 35) yellow to reddish-brown, made up of tough gelatinous layer on the outer walls of irregularly distorted and enlarged peripheral

<sup>&</sup>lt;sup>13</sup> The abbreviation "C. U." is used in this paper to designate the Herbarium of the Department of Plant Pathology, Cornell University.

cells, medulla (FIG. 46) tough, cartilaginous, paraplectenchymatous, center often prosoplectenchymatous with hyphae loosely interwoven, usually solid, very large sclerotia and sclerotial masses often hollow; sporophores (FIGS. 11, 47) filiform, erect, flexuous, straight or curved, apex usually acute, tapering below into a very long filiform stipe, not always well differentiated into stipe and clavula except at maturity, simple or branched, one or more (usually one) arising from any point on the sclerotium, sometimes arising directly from the mycelium, pubescent at the base, 20–100 mm. or more in length, translucent and shining when young, tawny to russet when mature, darker at the apex, whitish and opaque when dry; clavula straight or curved, cylindrical, elongate-fusiform, apex acute or rounded, 10-15 mm. long, 0.5-1.0 mm. in diameter, tawny to russet, tip sterile, darker, cinnoman-brown to Mars-brown, whitish when mature due to powdery layer of spores, hollow, subhymenium of small pseudoparenchymatous cells, densely crowded with coarse, dark-brown crystals which frequently obscure the origin of the basidia (FIG. 48), tissue below subhymenium also pseudoparenchymatous but of larger and looser cells, interior finally made up of loosely interwoven septate hyphae, or more often hollow; stipe distinct in size from clavula only at maturity, erect, flexuous, increasing gradually into clavula, pubescent only at base, 15–20 mm. long, 0.3–0.5 mm. in diameter, tawny to russet, shining when old or dry, solid or hollow, hyphae incrusted with dark crystals in parallel rows along the length of the stipe; basidia (FIG. 49) broad, cylindrical with very short stalk, rounded at the apex, four-spored,  $27-33 \mu \log_{10} 9-11 \mu \text{ in diameter}$ ; basidiospores (FIG. 53) ovoid to sub-fusiform, flattened on one side above a cylindrical apiculus,  $3.89-7.78 \times 9.73-13.62 \mu$ , average  $5.84 \times$ 11.64  $\mu$ .

HAB.: On overwintered leaves, petioles, herbaceous stems, grass, etc. Sclerotia are found in the spring, the sporophores arising in the autumn from the sclerotia or from the mycelium.

HERBARIUM SPECIMENS: C. U. 25233, 26950, N. Y., Mar.—Apr., on buckwheat straw; 27045, 27046, 27043, N. Y., Feb.—May, on *Acer* sp., *Alnus incana* and other leaves; 27042, N. Y., Mar., on corn fodder; 27044, N. Y., May, on *Solidago* sp. stems; 27047, N. Y., May, on lawn grass and overwintered leaves.

Notes: The fungus grows in culture from 0-21° C., with an optimum temperature of 12-15° C. Mycelial growth is appressed, granular, often concentrically banded and fan-shaped, forming a

rough cartilaginous mat over the surface of the agar. Sclerotia, which appear in 7–12 days, are very adherent to the surface of the agar, are clustered or in concentric rings, typically pyriform and flattened laterally, white at first, later russet to cinnamon-brown. Long sterile, yellowish-brown sporophores develop abundantly in culture from either sclerotia or the mycelium.

2. Typhula Itoana Imai, Trans. Sapporo Nat. Hist. Soc. 11: 39-44. 1929.

Material examined: C. U., Roum. Fungi Gall. 1400 Sclerotium fulvum Fries, Karsten's Herbarium Helsingfors, Finland: 14 Typhula graminum Karsten (type material) on leaves of Calamagrostis sp. and T. graminum Karsten on Polystichum spinulosum.

Sclerotia (FIG. 17) tawny to hazel-brown, immersed-erumpent, frequently falling away from substrate, single or coalesced, smooth at first, rough when dry or old, spherical to subglobose, often somewhat flattened or concave below and convex above, 0.5-2.0 by 1.5-4.0 mm.; rind (Fig. 30) golden to reddish-brown, about 7.78 \mu thick, tough, composed of a smooth gelatinous layer on the outer walls of enlarged peripheral cells; medulla (FIG. 42), paraplectenchymatous, center often prosoplectenchymatous with hyphae loosely interwoven, small sclerotia solid, large ones and coalesced masses often hollow; sporophores (FIG. 19) clavate, erect, straight or slightly curved, apex broad, round or slightly pointed, tapering into stipe, simple or branched, one or more (usually one) arising from each sclerotium, often slightly pubescent at the base, 8-25 mm. tall, clavula rose color, opaque, stipe white, translucent, becoming flesh color to bittersweet pink when dry; clavula straight, erect, smooth, cylindrical or somewhat broadened and flattened. tapering toward a round or slightly pointed apex, 10-15 mm. tall, 1-2 mm. broad, hydrangea pink to pale vinaceous-pink, made up of a hollow cylinder of agglutinated hyphae bearing the hymenium which is continuous over the apex, crystals present in the hymenium and subhymenium; stipe distinct in size and color from the clavula, erect, straight, pubescent at the base with hairs clasping the sclerotium, 5-10 mm. long, 0.5-1.0 mm. in diameter, white, solid, hyphae often slightly incrusted with fine crystals; basidia (FIG. 52) broadly clavate,  $27.23-34.62 \mu$  long,  $5.06-7.78 \mu$  wide; basidiospores (Fig. 56) ovoid, flattened on one side above a pointed apiculus, 4.28- $7.78 \times 11.29 - 14.78 \,\mu$ , average  $6.05 \times 11.71 \,\mu$ .

<sup>&</sup>lt;sup>14</sup> Lent to us through the courtesy of Dr. Harald Lindberg, Helsingfors, Finland.

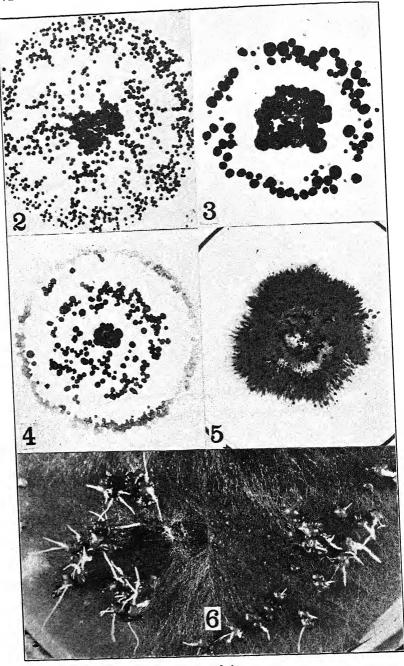
HAB.: Pathogenic on *Triticum*, *Hordeum*, *Phleum*, *Poa*, *Secale*, *Alopecurus*, and *Dactylis* sp. as well as saprogenic on herbaceous stems and leaves. Sclerotia are found in the spring after the snow melts, the sporophores arising from sclerotia in the autumn.

HERBARIUM SPECIMENS: C. U. 19192, 27211, 27212, 27213, 27214, 27215, 27216, 27217, 27218, N. Y., Feb.—June, 27219, Oct., 25211, 27100, Ida., Mar., on turf and lawn grass; 25236, N. Y., Mar., 27098, Ida., Mar., on Dactylis glomerata; 27099, 25154, Ida., Mar., 27095, Japan, May, on Hordeum sp.; 26156, Ida., Mar., 25155, Japan, May, on Triticum sp.; 27096, Japan, May, on Phleum sp.; 27097, Japan, Apr., on Alopecurus fulvus.

Notes: The fungus grows in culture at 0–18° C. with an optimum temperature of 9–12° C. Mycelial growth is abundant, white, webby, radiating, concentrically banded, and fan-shape. Sclerotia, which appear in 5–10 days, are pinkish orange when young and tawny to hazel brown when mature, single or coalesced with a tendency to develop in concentric rings. Sterile white sporophores frequently develop in culture from sclerotia (FIG. 6). A reddish-brown stromatic crust often develops in culture with small sclerotia arising on it.

This species causes a serious disease of cereals and grasses. It is sometimes collected with T. idahoensis, but more frequently occurs alone and more abundantly than that species. The name "snow-scald" has been applied to the disease caused by these two species (29) because of their association with snow and the scalded appearance of the plants after the snow melts. The disease occurs both under the snow and as the snow is melting. The plants are covered with a white mycelial growth and the tissue is filled with numerous reddish brown sclerotia.

There is a great deal of confusion in the literature concerning the nomenclature of *Typhula graminum*, *Sclerotium fulvum*, and *Typhula Itoana*. These names have all been applied to the organism causing the serious disease of cereals and grasses associated with snow and cold weather in the United States, Europe, and Japan. The writer has compared materials and cultures sent to her from Japan and Europe with the organism collected in the United States in the hope of clearing up this confusion.



Figs. 2-6.

Examination of cultures of the organism obtained from Japan,<sup>15</sup> showed the organism to be identical with the one occurring in the United States, both in sclerotial morphology and type of sporophores obtained from the sclerotia under natural and artificial conditions. This organism, therefore, is *Typhula Itoana* Imai.

Cultures <sup>16</sup> were obtained which causes the same type of disease in northern Europe, and which has been identified as *Typhula graminum* Karsten (36). An examination of these sclerotia, which were produced on potato dextrose agar, proved the sclerotial morphology to be identical with that of *Typhula Itoana* Imai. Sporophores have not yet been obtained from this material, and until they are available for comparison with those of *T. Itoana*, a definite synonymy cannot be made. Since the sporophores have been rarely observed in nature by European workers, and since the sclerotia resemble *Sclerotium fulvum* Fries in macroscopic morphology, it is easy to understand the prevalent usage of *Typhula graminum* Karsten as the causal organism of this disease of cereals.

An examination of Roumeguère, Fungi Gall. 1400, Sclerotium fulvum Fries, C. U., shows the sclerotium to be similar in macroscopic morphology and identical in microscopic morphology with that of T. Itoana. That is, the rind is a homogeneous gelatinous layer and the medulla paraplectenchymatous.

However, an examination of sclerotia from type material of *Typhula graminum* Karsten <sup>17</sup> shows the morphology of the sclerotium entirely different from that of *Sclerotium fulvum* and that of *T. Itoana*. That is, the medulla is prosoplectenchymatous with a layer of enlarged thin-walled cells adjacent to the homogeneous gelatinous rind. Furthermore, *T. graminum* is characterized by white sporophores, while *T. Itoana* has rose colored sporophores.

From these observations it appears that T. Itoana is a distinct

<sup>&</sup>lt;sup>15</sup> Sent to us through the courtesy of H. Tasugi, Tokyo, Japan.

<sup>&</sup>lt;sup>16</sup> Obtained through the courtesy of A. Volk, Königsberg, Germany.

<sup>&</sup>lt;sup>17</sup> Lent to us by Dr. Harald Lindberg, Helsingfors, Finland.

Figs. 2-6. Growth of five species of Typhula in culture on potato dextrose agar. 2-5, natural size; 6, × 2. 2, T. idahoensis, sclerotia formed singly and more or less clustered, 6° C.; 3, T. variabilis, sclerotia tending to coalesce, 6° C.; 4, T. gyrans, sclerotia in concentric rings, with outer ones immature, 9° C.; 5, T. intermedia, sclerotia upon brown stromatic crust, 18° C.; 6, T. Itoana, young sterile sporophores developing from the sclerotia, 6° C.

species from *T. graminum* based on morphological comparisons between the two. It seems unwise to draw this distinction too definitely, since the type material of *T. graminum* examined was old and fragmentary. It is advisable to obtain sclerotia of *Sclerotium fulvum* from the Fries collection to ascertain the morphology of the type material before a complete synonymy can be made.

### 3. Typhula sphaeroidea sp. nov.

Sclerotia colore ligno-brunneo paene usque ad nigrum, aliquantum aspera, innata, adhaerentia, simplicia v. acervatim, plana infra, convexa supra, saepe inaequalia, 0.5-1.0 mm., cortex aureus v. rubrus-brunneus, 15-30 \mu crassus, compositus e pluribus struibus paraplectenchymatosarum cellarum et extendens incomposite in medullam, medulla (FIG. 43) omnino paraplectenchymata v. hyphis centro laxe complexis quod centrum est cinctum atris et crassimuralibus cellis quasi interiorem corticem facientibus (FIG. 44); sporophori (FIGS. 23, 24) valde clavati v. subglobosi, recti, simplices, fere unus ex uno sclerotio v. orti directo ex myceliis, 1-3 mm. alti, albi, basi rubra-brunnea; clavula globosa, subglobosa v. pyriforma, 0.8-1.5 mm. longa, 0.5-1.5 mm. lata, colore cretae, dein lactea cum arescit, apice fertili, subhymenio incrustato; stipes distinctus, erectus, ad basem crassus, minutate pubescens, 1-2 mm. longus, 0.3-0.5 mm. diametro, albus, basi rubra-brunnea, solidus, incrustatus; basidia (FIG. 49) breva, crassa, abrumpentia, quadrispora, 19.45–45.01 μ longa, 9.73-11.67 \( \mu \) lata; basidiospori (Fig. 54) ovati, apiculo truncato manifesto,  $5.84-8.78 \times 11.67-13.62 \,\mu$ , modus  $6.69 \times 12.13 \,\mu$ .

HAB.: In mortuis caudicibus *Rubri* sp. Sporophoris collectis in mense Augusto ortis ex sclerotiis innatis in caudicibus.

Herbarium specimens: C. U. 26754, N. H., Aug., on dead stems of *Rubus* sp.

Notes: The fungus grows in culture from 0–25° C., with an optimum temperature of 12–18° C. Mycelial growth is white and appressed or webby. Sclerotia rarely develop in culture on potato dextrose agar. Fertile sporophores develop abundantly from mycelium on the surface of the agar from 12–18° C., are white with a reddish-brown base. Sterile, abnormal, white sporophores also develop in culture at 9–12° C.

4. TYPHULA GYRANS Batsch ex Fries, Obs. Myc. 2: 297–298. 1818.

Clavaria gyrans Batsch, Elenchus Fung. 235. pl. 28, f. 164a-e. 1783.

Clavaria granulata Willd. Florae 705. pl. 17, f. 17. 1787.

Cnasonaria setipes Corda, in Sturm, Deuts. Fl. Pilze 2: 55. pl. 25. 1829.

Clavaria trichopus Grev. Scott. Crypt. Fl. 1: 49. pl. 49. 1823. Clavaria setipes Grev. in Loudon, Encycl. 1012–1013. f. 16181. 1855.

Typhula stolonifera Quél. Assoc. Fr. Av. Sci. Compte Rendu 15: 506. pl. 12, f. 17. 1883.

ILLUSTRATIONS (in addition to the above): DeBary, Vergl. Morph. Pilze 35. f. 15 c. 1887; Pat. Tab. Anal. Fung. 1: 116. f. 262, 264. 1883.

MATERIAL EXAMINED: C. U., Roum. Fungi Gall. 3418 Typhula gyrans (Batsch) Fries.

Sclerotia natal-brown to clove-brown, nearly black when dry, immersed in substrate, single or coalesced into irregular masses, spherical to subglobose, usually flattened below and convex above, smooth at first, rough when dry, 0.5-3.0 mm. in diameter, shrinking somewhat with age and on drying; rind golden-brown to darkbrown, about 7.5 \( \mu \) thick made up of strata of hyphae winding around the medulla, surface view showing irregularly fused cells with hyphae running across the surface (FIG. 36), these hyphal layers breaking and sluffing away as the sclerotium matures and increases in size; medulla cartilaginous, paraplectenchymatous (FIG. 45), solid, center sometimes prosoplectenchymatous with hyphae loosely interwoven; sporophores (FIG. 12) clavate, erect to flexuous, twisted, simple, apex round or obtuse, one or more from each sclerotium, 5-15 mm. tall, milk-white, becoming pale olive-buff at maturity, reddish-brown at the base; clavula straight or slightly curved, cylindrical, fusoid or elliptical, 2-5 mm. long, 0.5-1.5 mm. broad, white to pale olive-buff, hollow, more or less filled with loosely interwoven hyphae sparingly incrusted with crystals, subhymenium somewhat more compact with hyphae thickly incrusted with these crystals, hymenuim extending over the apex; on drying, clavula bending down at an acute angle to the stipe, finally becoming parallel to it; stipe very distinct in size from the clavula, flexuous, twisted, weak, smooth at first, later pubescent, especially at base and just below the clavula, 10–16 mm. long, 0.1-1.25 mm. in diameter, fawn to walnut-brown at the base, becoming white above towards the clavula, solid, hyphae heavily incrusted with coarse crystals, especially towards the base, on drying twisting spirally at the top causing a characteristic gyrating movement of the clavula as it bends back parallel to it; basidia

elongate, blunt at the apex, four-spored, 7.78  $\mu$  broad, about 20–25  $\mu$  long; basidiospores (Fig. 57) obovate, flattened on one side above an inconspicuous pointed apiculus, 3.89–6.22  $\times$  8.56–11.67  $\mu$ , average 4.53  $\times$  10.03  $\mu$ .

HAB.: On dead leaves, petioles, and herbaceous stems on the ground. Sclerotia collected in the autumn.

HERBARIUM SPECIMENS: C. U. 25328, N. Y., Sept., on dead leaves; 27080, N. Y., Sept., on *Prunus serotina* leaves and petioles; 27092, N. Y., Sept., on *Rubus* sp. stems.

Notes: Because of its apparent resemblance to T. gyrans, Ty-phula stolonifera Quélet has been included here in the synonymy. Quélet noted this resemblance and thought it might be an abnormality of T. gyrans, since it arose from a brown stolon instead of a sclerotium. The Icones of Quélet and Patouillard show the plant to be identical with T. gyrans except for this character. This same phenomenon has been observed many times in these studies of Typhula, i.e., the sclerotium may produce a long stolon-like growth from which the sporophore will arise. The stipe itself may be prostrate for a distance before becoming erect due to obstacles in the substratum, thus resembling a stolon.

The fungus grows in culture over a range of 0–25° C. with an optimum temperature of 12–18° C. Mycelial growth is appressed or submerged, forming a cartilaginous mat on the surface of the agar. Sclerotia which appear in 7–14 days are single, rarely coalesced, scattered or in concentric rings (Fig. 4), white to light-buff when young, snuff-brown to clove-brown when mature. Brown stromatic crusts form on the surface of the agar at higher temperatures. Sterile sporophores have never been observed in culture.

## 5. Typhula Viburni sp. nov.

Sclerotia colore cinnamo brunneo usque ad Martem brunneum v. auburno usque ad castaneum brunneum, innataerumpentia, adhaerentia, simplicia v. acervatim, raro coalescentia, plana infra, convexa supra, glabra v. leviter aspera, 0.5–1.0 mm., cortex (fig. 34) aureus brunneus, 12–20  $\mu$  crassus, compositus e diversis struibus hypharum atrarum crassimuris implexarum, extremae cellae distortae et ruptae ut sclerotium crescit, medulla (fig. 45) cartilaginosa, pseudoparenchymatosa, centro saepe prosoplectenchymatoso, hyphis laxe complexis; sporophori (figs. 25, 26) clavati, erecti, recti v. leviter curvi, ad apicem crassi, attenuati infra, simplices, unus ex uno

sclerotio, glabri, 2–5 mm. alti, albi, suffusci ad basem; clavula recta v. curva, cylindrica, fusiforma-ellipsoidea v. ovata, 1.2–2.0 mm. longa, 0.5–1.0 mm. lata, alba, dein pallide brunnea, solida, hyphis laxe implexis, incrustatis, apice fertili; stipes distinctus, erectus, rectus minute pubescens, 4.0–4.5 mm. longus, 0.1–0.2 mm. diametro, albus, base brunnea, solidus, incrustatus; basidia elongata, apice retuso, quadrispora,  $20.0–23.5~\mu$  longa,  $7.78~\mu$  lata; basidiospori ovati, apiculo acuto,  $3.89–4.67~\times~7.78–9.73~\mu$ , modus  $4.38~\times~8.52~\mu$ .

HAB.: In mortuis foliis Viburni sp. Sporophoris collectis mense Augusto, orti e sclerotiis in foliis innatis.

HERBARIUM SPECIMENS: C. U. 26753, N. H., August, on dead leaves of *Viburnum* sp.

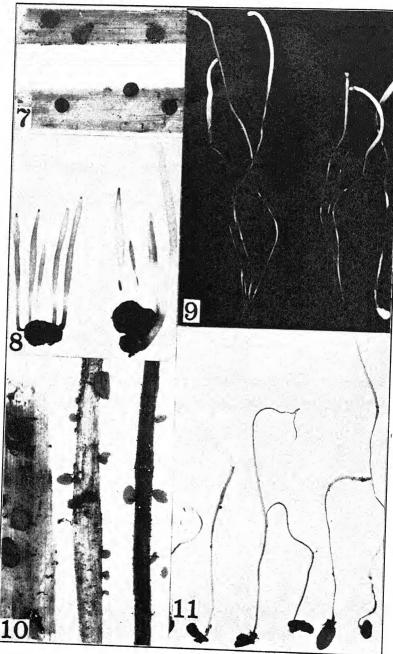
Notes: This species grows in culture from 0–27° C., with an optimum temperature of 12–18° C. Mycelial growth is appressed to submerged and hydrotic. Sclerotia, which appear in 7–14 days, are single or coalesced, in concentric rings, white to light-buff when young, cinnamon-brown to Mars-brown or chestnut-brown when mature. Stromatic crusts form at higher temperatures. Sterile sporophores frequently develop in culture from either sclerotia or mycelium.

### 6. Typhula umbrina sp. nov.

Sclerotia colore "van dyke" brunneo usque ad castaneum brunneum, dein propre ad nigrum cum arescunt, erumpentia v. superficia, semper simplicia, numquam acervatim, plana infra, convexa supra, glabra prima dein leviter aspera, 0.5-4.0 mm., cortex rubrus-brunneus, 7-12 \mu crassus, compositus e gelatinosa strue in exterioribus muris cellarum peripheralim amplificatarum angulatarum detorquearum (FIG. 33), medulla incrustata et prosoplectenchymata, cellis ad peripheriam amplificatis et tenuimuralibus et ad has adiacentibus cellis frequenter paraplectenchymatis (FIG. 39), centro solido; sporophori (FIG. 15) clavati, erecti, recti v. leviter curvi, crescenti gradatim ex tenui basi ad crassum apicem, simplices, unus v. plures ex uno sclerotio, basi minute pubescente, 8-15 mm. alti, albi, v. avellanei supra, hinnulei colore v. ligni brunnei infra; clavula cylindrica, gradatim attenuata e crasso apice in stipem, 3-8 mm. longa, 0.8-1.5 mm. crassa ad apicem, alba v. avellanea, solida, hyphis laxe complexis, incrustata, apice fertili; stipes distinctus, minute pubescens, capillis extensis ad basem, 3-4 mm. longus, 0.2-0.5 mm. diametro, himulei colore v. ligni brunnei v. "Rood "-brunneus, basi saepe aliquantum atriori, solidus, incrustatus; basidia elongata, quadrispora, 31.0-39.0 µ longa, 5.83–7.8  $\mu$  lata; basidiospori ovati, apiculo inmanifesto, 11.67–15.56  $\times$  3.89– 7.78  $\mu$ , modus 12.56  $\times$  5.54  $\mu$ .

HAB.: In rapis frigore conservatis et in iridum rhizomis.

HERBARIUM SPECIMENS: C. U. 25711, Br. Col., Apr., on turnips, 25710, Ottawa, Apr., on leaves and rhizomes of iris.



Figs. 7-11.

Notes: The two collections of this fungus were obtained from Dr. F. L. Drayton, Ottawa, Canada, who observes that the organism apparently causes a mild necrosis of suscept tissue. The optimum temperature of the fungus (6–12° C.) indicates that its activity is confined to low temperatures, and it is possible that it is weakly pathogenic.

The fungus grows in culture over a range of 0–18° C. with an optimum temperature of 6–12° C. Mycelial growth is radiating, appressed, somewhat granular and concentrically banded. Sclerotia, which appear in 5–7 days, are always single and never coalesced, have a tendency to form in concentric rings at low temperatures, and to cluster closely together at higher temperatures, are light yellow to tan when young, chestnut brown when mature. No sterile sporophores have been observed in culture.

7. TYPHULA VARIABILIS Riess, Hedwigia 1: 21. pl. 3, f. 2c. 1853.

Lycoperdon Brassicae Bergius, Sv. Vet. Acad. Handl. 26: 213. 1765.

Tremella sphaerica Gleditsch, Ver. Phys. Bot. Oecon. Abhandl. 2: 346. 1766.

Lycoperdon subterraneum Haller, Historia 3: 120. 1768.

Lycoperdon minimum Murray, Comm. Gotting. 3:83. 1772.

Lycoperdon oleraceum Pollich, Hist. Pl. 3: 314. 1777.

Sphaeria Brassicae Dickson, Fasc. Plant Crypt. Brit. 1: 23. 1785.

Sclerotium semen Tode, Fungi Meckl. 1: 4. pl. 1, f. 6a-c. 1790.

Sclerotium semen (Tode) var. Brassicae (Bergius) Fries, Syst. Myc. 2: 249. 1822.

Typhula lactea Tul. Sel. Fung. Carp. 1: 106. 1861.

Typhula semen (Tode) Quél. Bull. Soc. Myc. Fr. 24: 326. pl. 6, f. 2. 1877.

Figs. 7-11. Sclerotia and sporophores of two species of Typhula. All  $\times$  2. 7, sclerotia of T. variabilis on herbaceous stems; 8, young sporophores of T. variabilis arising from artificially grown sclerotial masses in diffused daylight; 9, mature sporophores of T. variabilis produced under ultra-violet irradiation; 10, sclerotia of T. phacorrhiza showing natural habitat on herbaceous stems; 11, mature sporophores of T. phacorrhiza arising from single sclerotia in diffused daylight.

ILLUSTRATIONS (in addition to the above): Brefeld, Unters. Gesammt. Myk. 3: pl. 8, f. 1–3. 1877; Bolton, Hist. Fung. pl. 119, f. 1–2. 1789; Britz. Hymen. Südb. 5: pl. 741, f. 42. 1885; Corda, Ic. Fung. 3: pl. 3, f. 55. 1839; Henn., in E. & P., Nat. Pfl. 1: f. 71m–n. 1900; Herter, Krypt. der Mark Brandenburg 6: f. 16 and 147, f. 2a–c. 1910; Neveu-Lemaire, Parasit. Pl. Agric. f. 194. 1913; Prilleux, Malad. Pl. Agric. 1: f. 119, 120. 1895; Sow. Engl. Fungi 3: pl. 393, f. 3. 1803; Winter, in Rab. Krypt.-Fl. 1: 301, 293. f. 3–4. 1884; Zopf, Pilze f. 79a–b. 1890.

MATERIAL EXAMINED: C. U., Krieger, Fungi Sax. 478; H. Sydow, Myc. Germ. 1200.

Sclerotia (FIG. 7) resembling large mustard seeds, chestnutbrown to almost black, free on surface of substrate, single or coalesced, smooth at first, becoming rough or furrowed, especially when dry or after fruiting, spherical to somewhat flattened, convex on top, flat or concave below, indented at point of attachment of the minute stalk, falling away from the substrate easily when mature, 3-5 by 5-6 mm., rind dark-reddish-brown, 10-15  $\mu$  thick, composed of a rough, gelatinous layer on the outer walls of large, irregular and distorted, peripheral cells, medulla prosoplectenchymatous, with cells adjacent to rind enlarged and thin-walled, solid, center either compact or of loosely interwoven hyphae; sporophores (FIGS. 8, 9, 50) clavate, erect, straight or slightly curved, apex acute, tapering below into a slender stipe, simple or branched, one or more arising from each sclerotium, hairy at base, 30-50 mm. tall, olive-buff to smoke-grey, darker at the apex and base, avellaneous to wood-brown when dry or with age, sclerotia forming over surface of old sporophores under moist conditions: clavula cylindrical or somewhat flattened, often longitudinally furrowed, spores frequently collect in balls over the surface giving a warted appearance, 10-20 mm. long, 1-3 mm. broad, olive-buff, tip sterile, darker, of a light greyish-olive, this darker tip very characteristic even in young developing sporophores, old specimens often proliferating to form spur-like branches, hollow, more or less filled with very loosely interwoven septate hyphae, sparingly incrusted with large crystals, subhymenium of compact hyphae, thickly incrusted with these crystals; stipe very distinct in size and color from clavula, minutely pubescent when mature with spreading bristly hairs at the base which clasp the sclerotium, 5-25 mm. long, 0.5-1.0 mm. in diameter, smoke-grey at base and gradually becoming lighter upwards, almost shiny white just below clavula, silky when old or dry, solid, hyphae somewhat incrusted; basidia (FIG. 51) elongate, round at apex, four-spored, 27.23  $\mu$  long, 7.78  $\mu$  wide, a clamp connection at the base of each basidium; basidiospores (FIG. 55) ellipsoid-fusiform, flattened or slightly incurved on one side above the conical apiculus,  $3.89-5.84 \times 10.67-15.56 \,\mu$ , average  $4.3 \times 11.39 \,\mu$ .

HAB.: On vegetables in cold storage or on overwintered corn fodder, buckwheat straw and various herbaceous stems, leaves, and petioles on the ground. Sclerotia are found in the spring, the sporophores in the autumn, arising from the sclerotia.

Herbarium specimens: C. U. 26952, N. Y., Mar.—Apr., on buckwheat straw; 2183, 5185, 14459, 27031, N. Y., Mar.—Apr., on corn stalks and leaves; 5184, 16401, 25666, 27033, N. Y. and Ottawa, Jan.—Apr., on herbaceous stems and leaves; 27030, 27032, N. Y. and Montreal, Dec.—Apr., on celery in cold storage; 12256, Mo., Sept., with clover seed.

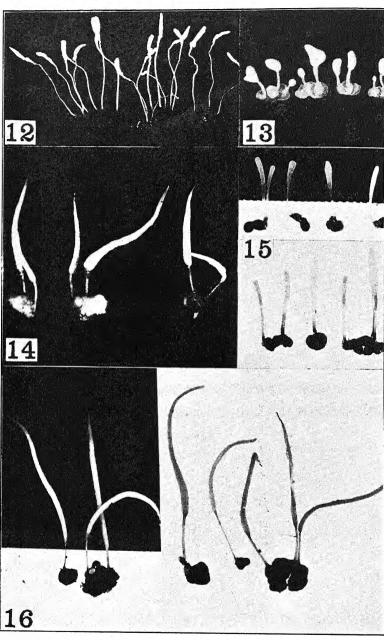
Notes: A very destructive disease of sugar beets and potatoes caused by *T. variabilis* has been reported a number of times from European countries and from the Azores (2, 7, 22, 27, 31, 35). It has also been reported weakly pathogenic on stored celery at the University of Montreal and at Cornell University. Artificial inoculation experiments have produced infections on beets, potatoes, asparagus rhizomes and stored celery (l. c.).

Growth in culture occurs over a range of 0–21° C. with an optimum temperature 12–15° C. Mycelial growth is appressed, woolly to powdery and inconspicuous. Sclerotia are produced in 7–14 days, are single or coalesced into masses (FIG. 3), white when young, mahogany-red to chestnut-brown when mature. At 21° C. a brown stromatic crust is formed over which a few, small sclerotia develop in concentric rings. Sterile white sporophores occasionally develop in culture.

## 8. Typhula virgata sp. nov.

Sclerotia colore verono-brunneo, innata-erumpentia, simplicia v. frequenter acervatium, globosa v. subglobosa v. plana, 0.5-0.8 mm., cortex aureus brun-

<sup>18</sup> Robert White-Stevens, Department of Vegetable Crops, Cornell University. (Unpublished.)



Frgs. 12-16.

neus,  $5-10\,\mu$  crassus, compositus e gelatinosa strue in exterioribus muris cellarum peripheralium incompositarum amplificatarum, medulla prosoplectenchymata, cellis adiacentibus ad corticem amplificatis et tenuimuralibus praeditis, centro solido, hyphis laxe complexis; sporophori (FIG. 21) virgati, cylindrici, recti v. leviter curvi, ad apicem rotundi v. crassi, decrescentes gradatim deorsum, simplices, fere unus ex uno sclerotio sive e mycelio sive e stromaticis crustis, 4–12 mm. alti, toti albi; clavula recta v. curva, filiforma v. crassa, obtusa v. rotunda ad apicem, 5–11 mm. longa, 1.5 mm. lata, solida, hyphis incrustatis, apice fertili; stipes indistinctus praeterquam ad maturitam, rectus v. curvus, minute pubescens, 2–6 mm. longus, 0.1–0.2 mm. diametro, solidus, aliquantum incrustatus; basidia elongata, bi- v. quadrispora (FIG. 1, b, c) 25–30  $\mu$  longa, 5.8–7.8  $\mu$  lata; basidiospori ellipsoidei, apiculo acuto, 3.89–5.84  $\times$  9.27–15.17  $\mu$ , modus 4.26  $\times$  12.24  $\mu$ .

HAB.: In hibernatis herbaceis caudicibus. Sporophoris ortis in autumno ex sclerotiis innatis in caudicibus.

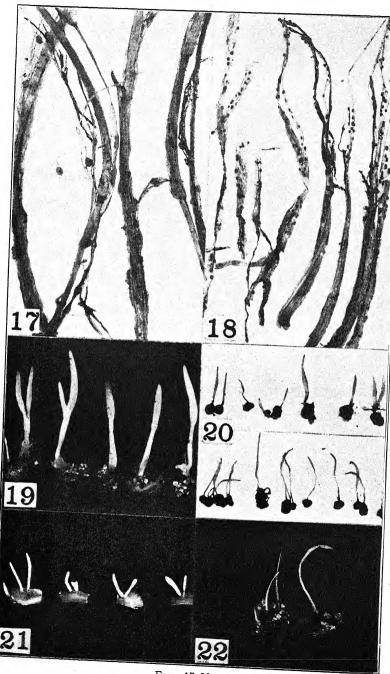
HERBARIUM SPECIMENS: C. U. 25158, N. Y., Sept., on overwintered herbaceous stems.

Notes: The fungus grows in culture from 0–21° C. with an optimum temperature of 12–15° C. Mycelial growth is thin and hydrotic at first, later forming dark, tough, irregular stromatic crusts. Sclerotia, which appear in 7–12 days, are single or coalesced, single at 15–18° C., spherical or irregular, flat or concave below and convex above, white to light-buff when young, veronabrown when mature. No sterile sporophores have been observed in culture.

## 9. Typhula pertenuis sp. nov.

Sclerotia colore "bister" prope ad nigrum, superficia, simplicia v. acervatim, glabra dein aspera globosis v. subglobosis, 2–3 mm., cortex valde aureus brunneus,  $7-10\,\mu$  crassus, compositus ex aspera et gelatinosa strue in exterioribus muris cellarum peripheralium amplificatarum incompositarum detroquearum, medulla prosoplectenchymata, cellis adiacentibus ad corticem amplificatis et tenuibus muris praeditis, centro solido, hyphis laxe complexis;

Figs. 12-16. Sporophores of five species of Typhula from artificially grown sclerotia. All  $\times$  2. 12, T. gyrans from sclerotial masses under ultra-violet light; 13, T. latissima from sclerotial masses in diffused daylight; 14, T. subulata from sclerotial masses in diffused daylight; 15, T. umbrina from single sclerotia in diffused daylight; 16, T. intermedia from sclerotial masses in diffused daylight, those on the right showing method of clavula branching in old specimens.



Figs. 17-22.

sporophores (FIG. 22) elongati-clavati, tenuissima, erecti v. nonnihil prosterni, rotundi ad apicem, attenuati infra, simplices, fere unus ex uno sclerotio, sive orientes e mycelio sive e stromaticis crustis, 6–30 mm. alti, toti albi dein avellanei cum senescunt v. arescunt; clavula recta v. curva, rotunda ad apicem, 8–15 mm. longa, 1.0–3.0 mm. lata, solida, hyphis aliquantum incrustatis, apice fertili v. sterili; stipes distinctus, rectus v. curvus, pubescens, 4–10 mm. longus, 0.5–1.5 mm. diametro, solidus, aliquanutm incrustatus; basidia elongata, quadrispora, circiter 25  $\mu$  longa, 7.78  $\mu$  lata; basidiospori ovati, apiculo acuto, 3.89–5.84  $\times$  7.78–12.45  $\mu$ , modus 4.9  $\times$  9.18  $\mu$ .

HAB.: Per humum. Sporophoris collectis in autumno orti e sclerotiis.

HERBARIUM SPECIMENS: C. U. 27284, N. Y., Sept., on soil.

Notes: The fungus grows in culture from 0–21° C., with an optimum temperature of 15–18° C. Mycelial growth is white, granular or webby, and brown stromatic crusts develop on the surface of the agar at 15–21° C. Sclerotia, which appear in 5–7 days, are white when young, bister when mature, are single, clustered, or frequently coalesced and irregular, convex above, flat or concave below. Sterile sporophores have never been observed in culture.

10. Typhula intermedia Appel & Laubert, Arb. Anst. Landw. Forstwirtsch. 5: 153. 1905.

Sclerotia mahogany-red to chestnut-brown or van dyke-brown to nearly black, superficial or erumpent on substrate, always single, never coalesced, smooth and glistening when moist, rough and dull when dry, spherical to sub-globose, falling away from substrate when mature,  $0.5-1.0 \times 1.5-3.5$  mm., rind (FIG. 37) very dark reddish-brown, golden toward the medulla,  $11-15~\mu$  thick, composed of a rough tuberculate gelatinous layer on the outer walls of irregular and distorted peripheral cells, in surface view the tubercles appear in rosettes, medulla (FIG. 41) prosoplectenchymatous, solid, with hyphae often more loosely interwoven in the center; sporophores (FIG. 16) clavate, erect to flexuous, frequently prostrate,

Figs. 17-22. Sclerotia and sporophores of four species of Typhula. 17, 19-22, × 2; 18, natural size. 17, sclerotia of T. Itoana embedded in tissue of Dactylis glomerata; 18, sclerotia of T. idahoensis embedded in tissue of Agropyron cristatum; 19, sporophores of T. Itoana arising from artificially grown sclerotial masses in diffused daylight; 20, sporophores of T. idahoensis arising from single sclerotia in diffused daylight; 21, sporophores of T. virgata arising from mycelial masses on surface of agar in diffused daylight; 22, sporophores of T. pertenuis arising from sclerotia in diffused daylight.



Figs. 23-28.

simple, one or more from each sclerotium, 18–40 mm. tall, entirely white, sterile, filiform, branched sporophores often arising from the sclerotia instead of the normal clavate ones; clavula straight to slightly curved, cylindrical, tapering at the apex, 6–20 mm. long, 0.5–1.0 mm. in diameter, hollow, made up of loosely interwoven hyphae incrusted with crystals, hymenium continuous over apex; stipe distinct in size from clavula, weak, rarely erect, usually flexuous or prostrate from weight of clavula, somewhat pubescent, 5–15 mm. long, 0.3–1.0 mm. in diameter, solid, hyphae incrusted with crystals; basidia elongate, slender, four-spored, 25–30  $\mu$  long, 9–10  $\mu$  wide at the apex; basidiospores ellipsoid, flattened on one side above a prominent pointed apiculus, 11.67–15.95  $\times$  4.28–7.78  $\mu$ , average 13.88  $\times$  6.19  $\mu$ .

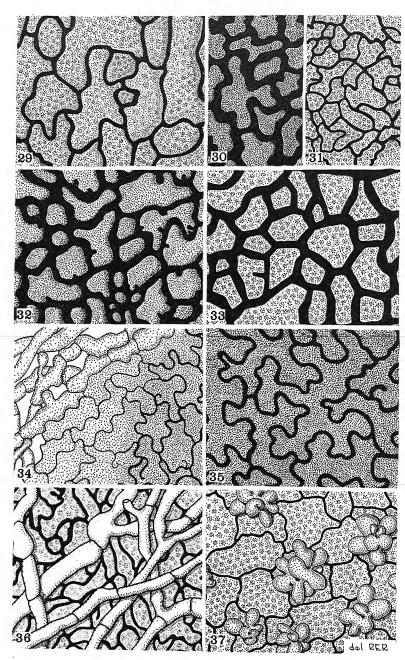
HAB.: On fallen overwintered leaves, petioles, and herbaceous stems. Sclerotia are found in the spring, the sporophores in the autumn arising from the sclerotia.

HERBARIUM SPECIMENS: C. U. 25234, N. Y., Mar., on herbaceous stems; 26951, N. Y., Apr., on buckwheat straw; 25235, N. Y., Feb.–Mar., on *Populus* sp. and *Acer* sp. leaves.

Notes: A very striking character of *T. intermedia* is the frequent production of sterile, white, filiform, branched sporophores from the sclerotia instead of the usual clavate fertile sporophores. This character is given particular attention by Appel and Laubert in their original description of the species. This tendency to produce sterile sporophores is particularly apparent under ultra-violet irradiation.

The fungus grows in culture over a range of 0–21° C., with an optimum temperature of 12–15° C. Mycelial growth is fan-shape and woolly. Sclerotia which appear in 7–14 days, are always single, never coalesced, white when young, chestnut-brown to van dyke-brown when mature. A brown stromatic crust is formed at 15–21° C. over which a few small sclerotia develop. Sterile white sporophores are frequent in culture from 6–15° C.

Figs. 23–28. Sporophores of three species of *Typhula* arising from sclerotia embedded in the natural substrate, 23, 25, 27, and from artificially grown sclerotial masses, 24, 26, 28. All × 2. 23, *T. sphaeroidea* on stems of *Rubus* sp.; 24, *T. sphaeroidea* produced under ultra-violet irradiation; 25, *T. Viburni* on leaves of *Viburnum cassinoides*; 26, *T. Viburni* produced under ultra-violet irradiation; 27, *T. Athyrii* on stems of *Athyrium angustum*; 28, *T. Athyrii* produced in diffused daylight.



Figs. 29-37.

### 11. Typhula idahoensis sp. nov.

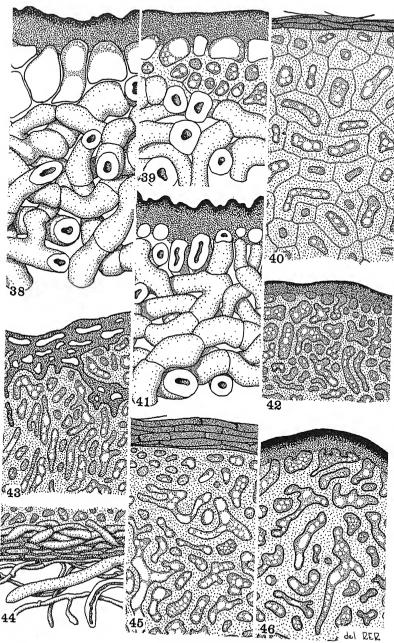
Sclerotia (FIG. 18) colore castaneo brunneo v. ossibrunneo paene usque ad nigrum, innata dein erumpentia v. superficia, semper simplicia, nunquam acervatim, globosa v. subglobosa, plana infra, convexa supra, glabra, nitida dein obscura,  $0.5-0.9 \times 1-2$  mm., cortex valde rubrus-brunneus,  $5-20 \mu$  crassus, compositus e gelatinosa strue in exterioribus muris cellarum peripheralium incompositarum amplificatarum (FIG. 29), medulla omnino prosoplectenchymata, centro solido, hyphis laxe complexis; sporophori (FIG. 20) clavati, erecti, recti v. leviter curvi, simplices v. raro ramosi, glabri, ad apicem crassi, rotundi v. acuti, unus v. plures ex uno sclerotio, sive orientes directo e mycelio, sive e stolonibus orits e sclerotiis et crescentibus per superficiem humi, 5-10 mm. alti, hinnulei colore v. ligni brunnei, clavula stipe pallidior; clavula recta, elongata-fusiforma, cylindrica, saepe crassa ad apicem, 4-7 mm. longa, 0.5-1.5 mm. lata, vinacea-brunnea v. hinnulea- v. lignea-brunnea, apice atriori, inanis seu hyphis laxe complexis, incrustata, apice sterili seu fertili; stipes distinctus, rectus v. aliquantum flexilis, glabrus v. leviter pubescens ad basim, 2-5 mm. longus, 0.1-0.5 mm. diametro, bistri colore v. umbri v. brunnei "van dyke," solidus, incrustatus; basidia elongata, crassa ad apicem, cellis confibula coniunctis ad basem, quadri- sexti- v. octospora (FIG. 1, c-e), 27.0-31.5  $\mu$  longa, 5.8-7.78  $\mu$  lata; basidiospori ovati v. ellipsoidei, apiculo inmanifesto,  $3.8-7.78 \times 8.17-13.61 \,\mu$ , modus  $4.55 \times 10.51 \,\mu$ . HAB.: Pathogeniti in foliis et caudicibus Tritici vulgaris et Agropyri

cristati. Sclerotiis vere collectis post nives solutas, sporophoris in autumno ortis ex sclerotiis.

HERBARIUM SPECIMENS: C. U. 25316, 27220, 27221, 27222, Ida., Apr.-May, 25153, Mont., Apr., on Triticum vulgare; 27223, Ida., May, on Agropyron cristatum.

Notes: The organism grows in culture over a range of 0–18° C., with an optimum temperature of 9-12° C. Mycelial growth is abundant, fluffy and concentrically banded. Sclerotia, which appear in 5–10 days, are clustered or in concentric rings, always single, never coalesced into masses (FIG. 2), light-amber when young, chestnut-brown when mature. Sterile brown sporophores develop from sclerotia abundantly in culture.

Figs. 29-37. Surface views of sclerotia of nine species of Typhula showing characteristic morphology of peripheral cells composing the rind. All × 450. 29, irregular thin-walled cells of T. idahoensis; 30, irregular thickwalled cells of T. Itoana; 31, very small irregular cells of T. Athyrii; 32. irregular thick-walled cells of T. variabilis; 33, angularly thickened walls of T. umbrina; 34, young sclerotium of T. Viburni showing the development from loosely intertwined distinct hyphae to fused thick-walled cells composing the mature rind; 35, very irregularly distorter peripheral cells of T. phacorrhisa; 36, mature rind of T. gyrans with adhering intertwining peripheral hyphae; 37, tuberculate rind of T. intermedia.



Figs. 38-46.

This species causes a disease of cereals and grasses similar to that caused by *T. Itoana*. Sclerotia of the two fungi are often collected in the same field but are readily distinguished by their color.

### 12. Typhula Athyrii sp. nov.

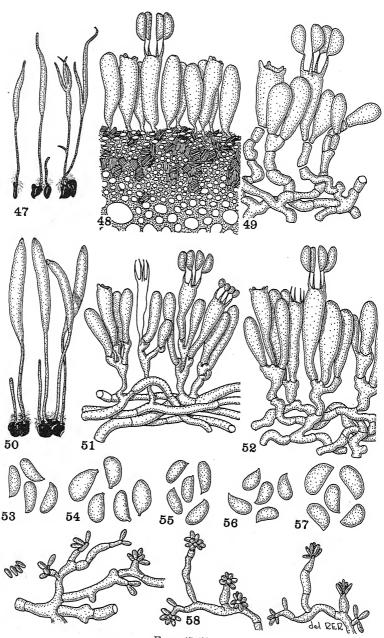
Sclerotia colore argillaceo usque ad fulvum olivem v. gayrophyllono brunneo, innata-erumpentia, simplicia v. acervatim, globoso v. elongata, convexa supra, plana v. concava infra,  $0.5-0.7 \times 1.0-1.5$  mm., cortex aureus flavus, 7-10 \( \mu\) crassus, compositus ex aspera et gelatinosa strue in exterioribus muris cellarum peripheralim leviter amplificatarum (FIG. 31), medulla incrustata omnino prosoplectenchymata, centro solido, hyphis laxe complexis; sporophori (FIGS. 27-28) clavati, erecti v. flexiles, recti v. leviter curvis, ad apicem rotundi, attenuati infra, simplices v. frequenter ramosissimi, basi pubescente, unus v. plures ex uno sclerotio, sive orientes e stromaticis crustis, 4-15 mm. alti, toti albi, dein sublutacei cum senescunt v. arescunt; clavula cylindrica, recta v. curva, 3-7 mm. longa, 0.5-2.5 mm. lata, solida, apice fertili, hymenio incrustato; stipes distinctus, rectus v. curvus, minute pubescens, 2-5 mm. longus, 0.5-1.0 mm. diametro, gradatim crescens in clavulam, non incrustatus; basidia elongata, quadrispora, circiter 30 \mu longa, 8 \mu lata; basidiospori fusiformi-ellipsoidei, apiculo acuto, 3.89-5.8 × 7.78-2.84 \( \mu \) modus 4.12  $\times$  11.06  $\mu$ .

HAB.: In hibernatis caudicibus Athyrii angusti. Sporophoris collectis autumno orti e sclerotiis.

HERBARIUM SPECIMENS: C. U. 24900, N. Y., Sept., on Athyrium angustum.

Notes: The fungus grows in culture over a range of 0–25° C., with an optimum temperature of 18–21° C. Mycelial growth is appressed and scanty. Sclerotia, which appear in 5–10 days, are single or coalesced, white to light-buff when young, clay to tawny-olive when mature. Brown stromatic crusts are frequent in culture. Sterile sporophores have never been observed in culture.

Figs. 38-46. Sections through sclerotia of eight species of Typhula showing morphology of medulla and rind. All × 450. 38, prosoplectenchymatous medulla and row of enlarged thin-walled cells adjacent to gelatinous rind of T. variabilis; 39, T. umbrina with interior of sclerotium prosoplectenchymatous and outer portion paraplectenchymatous with enlarged thin-walled hyphae adjacent to gelatinous rind; 40, T. Viburni with medulla pseudoparenchymatous and rind made up of intertwining peripheral hyphae; 41, prosoplectenchymatous medulla and gelatinous rind of T. intermedia; 42, paraplectenchymatous medulla and homogeneous gelatinous rind of T. Itoana; 43 and 44, periphery and center of T. sphaeroidea showing paraplectenchymatous medulla and rind with center of sclerotium bounded by an inner rind-like area; 45, paraplectenchymatous medulla and rind of intertwining peripheral hyphae of T. gyrans; 46, paraplectenchymatous medulla and homogeneous rind of T. phaeorrhisa.



Figs. 47-58.

### 13. **Typhula latissima** sp. nov.

Sclerotia colore ossibrunneo, innata-erumpentia, simplicia v. acervatim, globosa v. subglobosa v. plana et inaequalia,  $1.5-2.5 \times 2.5-3.0$  mm., cortex valde rubrus-brunneus,  $10-15~\mu$  crassus, compositus ex aspera et gelatinosa strue in exterioribus et inaequalibus muris amplificatarum peripheralium cellarum, medulla omnino prosoplectenchymata, centro solido, hyphis laxe complexis; sporophori (Fig. 13) clavati, erecti v. flexiles, rotundi v. crassi ad apicem, statim in tenues stipes decrescentes, simplices, unus v. plures ex uno sclerotio, 6-18 mm. alti, colore albo v. palide olivo-brunneo, dein sublutacei ut senescunt aut arescunt; clavula recta v. curva, cylindrica v. subglobosa v. plana, rotunda ad apicem, 4-8 mm. longa, 0.8-2.0 mm. lata, colore albo v. pallide olivo-brunneo, nigrescens ut senescit, solida, hyphis incrustatis, ad apicem fertilis; stipes distinctissimus, erectus v. flexilis, pubescens, basi crassa, 3-10 mm. longus, 0.1-0.5 mm. diametro, solidus, hyphis nonnihil incrustatis; basidia elongata, quadrispora, circiter  $30~\mu$  longa,  $8~\mu$  lata; basidiospori ovati, apiculo acuto,  $3.89-7.78 \times 9.72-15.17~\mu$  modus  $4.12 \times 10.66~\mu$ .

HAB.: In hibernatis caudicibus *Typhae latifoliae*. Sporophoris collectis in autumno ortis ex sclerotiis.

HERBARIUM SPECIMENS: C. U. 25157, N. Y., Sept., on Typha latifolia.

Notes: The fungus grows in culture from 0–25° C. with an optimum temperature of 12–15° C. Mycelial growth is scanty and appressed, and dark stromatic crusts form at all temperatures. Sclerotia which appear in 5–10 days, show a strong tendency to coalesce, are light-buff when young, army-brown to bone-brown when mature. No sterile sporophores have been observed in culture.

Figs. 47–58. Sporophores, basidia, basidiospores, and microconidia of five species of Typhula. 47 and 50 natural size; 48, 49, 51–58 × 450. 47, habit sketch of sporophores of T. phacorrhiza arising from single sclerotia; 48, section through clavula of T. phacorrhiza showing cylindrical basidia arising from a pseudoparenchymatous subhymenial layer heavily incrusted with dark crystals; 49, fragmentation of basidial and hyphal cells of T. sphacroidea; 50, habit sketch of sporophores of T. variabilis arising from single sclerotia; 51, basidia of T. variabilis showing clamp connections at the base of each basidium; 52, basidia of T. Itoana showing broadened basal cells without clamp connections; 53, fusiform spores with pointed apiculus of T. phacorrhiza; 54, ovoid spores with truncate apiculus of T. sphacroidea; 55, ovoid spores with obconical apiculus of T. variabilis; 56, ovoid spores with pointed apiculus of T. Itoana; 57, ovoid spores with inconspicuous apiculus of T. gyrans; 58, microconidia of T. Itoana arising from lateral branches on old mycelium.

### 14. Typhula subulata sp. nov.

Sclerotia colore sternutamenti brunneo, innata-erumpentia, simplicia v. frequenter acervatim, globosa v. elongata, plana infra, convexa supra, glabra dein aspera aut arescunt,  $2.0\text{--}2.5 \times 2.0\text{--}2.8$  mm., cortex aureus brunneus,  $10\text{--}15\,\mu$  crassus, compositus ex aspera et gelatinosa strue in exterioribus muris cellarum peripheralium leviter amplificatarum, medulla omnino prosoplectenchymatosa, centro solido, hyphis laxe complexis; sporophori subulati (Fig. 14), acutissimi, recti usque ad curvi, simplices, unus ad tres ex uno sclerotio, 9–18 mm. alti, colore pallidulo v. plane pallido, stipes colore atrior; clavula recta v. leviter curva, latissima ad basem, diminuens in acutissimum sterilem apicem, 8–13 mm. longa, 0.5–2.0 mm. lata, colore pallidulo v. plane pallido, solida, hyphis laxe complexis et incrustatis; stipes distinctus, glabrus, 3–5 mm. longus, 0.1–0.2 mm. diametro, colore leviter brunneo (anglice "buff") usque ad ligni brunneum, solidus, nonnihil incrustatus; basidia elongata, quadrispora, circiter 30  $\mu$  longa, 8  $\mu$  lata; basidiospori ellipsoidei, apicula acuto,  $7.0\text{--}7.78 \times 12.45\text{--}15.56\,\mu$ , modus  $7.37 \times 13.85\,\mu$ .

HAB.: In mortuis foliis et herbis in autumno. Sclerotiis in autumno

collectis.

HERBARIUM SPECIMENS: C. U. 25159, Manitoba, Sept., on dead leaves and grass.

Notes: The fungus grows in culture from 0–21° C., with an optimum temperature of 12–15° C. Mycelial growth is abundant, coarse and concentrically banded at 18–21° C. Sclerotia, which appear in 5–7 days, are single or coalesced, in concentric rings, white when young, snuff-brown when mature. Sterile brown sporophores frequently develop in culture from sclerotia or myceliae mats. Stromatic crusts appear on the surface of the agar at temperatures of 12° C. or above.

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# EXPLANATION OF FIGURES

All drawings were made with the aid of a camera lucida. The photographs were made by W. R. Fisher, photographer for the Plant Pathology Department, Cornell University.

## CULTURAL AND GENETICAL STUDIES OF CERTAIN AGARICS <sup>1</sup>

JOHN B. ROUTIEN

This paper deals with studies of certain Agarics for the purpose of finding a medium upon which they would form typical fruiting-bodies and to determine the type of "sexuality" possessed by each species.

#### CULTURAL STUDIES

#### Materials and methods

Tissue cultures were secured of the following species: <sup>2</sup> Coprinus atramentarius Fries, C. comatus Fries, C. fimetarius macrorhizus Fries, C. micaceus Fries, C. plicatilis Fries, C. quadrifidus Peck, C. radians Fries, C. radiatus Fries, C. semilantanus Peck, Galera crispa Longyear, G. tenera (Fries) Quél., Panaeolus campanulatus (Fries) Quél., P. retirugis (Fries) Quél., P. solidipes (Fries) Quél., Psilocybe subviscida Peck, Stropharia semiglobata (Fries) Quél.

The stock cultures of these fungi were grown on potato maltextract agar, and transfers were made from this to the eightyseven media that were tested either in test-tubes or Erlenmeyer flasks for their value for the growth of the fungi and the production of fruiting-bodies.

There were five general types of media: those consisting of more or less unchanged, natural substances; those containing some known carbohydrate for the food supply; those consisting of potato malt-extract agar to which were added poisons or weak antiseptics; those consisting of potato malt-extract agar to which

<sup>1</sup> This is an abbreviated form of a thesis submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy in the Department of Botany of Michigan State College.

<sup>2</sup> Coprimus fimetarius macrorhisus Fries and the species described by Peck and Longyear have the author citations that are given by Kauffman (12). The works of Fries (5, 6, 7, 8, 9), Gillet (10), Karsten (11), and Quélet (13) were used to determine the authors for the other species.

"growth-promoting" substances were added; and those which were treated in some manner to modify the physical conditions.

#### RESULTS

On the following media the growth was very poor or entirely lacking: decayed wood, sawdust, horse-dung, grass, horse-dung straw mixture, sand horse-dung decayed cottonwood, dung-extract agar, potatoes, malt peptone agar, dung-extract potato malt agar, modifications of Clausen's, Leonian's, Tubeuf's, Duggar's and Piefer, Humphrey and Acree's agar media, potato raffinose agar, potato mannose agar, sucrose corn-starch agar, Czapek's glycerine agar, oatmeal agar, and some of the media that were treated to obtain a change in the physical conditions.

Typical fruiting-bodies of a number of the species were formed on the following media: straw malt-extract, straw potato maltextract, potato malt-extract agar, potato glucose agar.

The modification of Etter's medium (4) was good for the production of fruiting-bodies only of Coprinus quadrifidus. Dung-extract agar was good only for C. radians, C. semilantanus, Panacolus campanulatus and Stropharia semiglobata.

The following species did not form fruiting-bodies on any of the media upon which they were grown: Coprinus atramentarius, C. comatus, C. plicatilis, Galera crispa, G. tenera, Psilocybe subviscida.

It was observed in all of the species that produced fruiting-bodies that the most typical sporophores were the first ones that developed after the fungus was secured in culture. As the age of culture of the fungus increased, the ability to form fruiting-bodies decreased. The rate of decline of this capacity varied with the different species.

### DISCUSSION AND CONCLUSIONS

The following species formed fruiting-bodies on one or more media: Coprinus fimentarius macrorhizus, C. micaceus, C. quadrifidus, C. radians, C. radiatus, C. semilantanus, Panaeolus campanulatus, P. retirugis, P. solidipes and Stropharia semiglobata.

The media that were most valuable for sporophore production were straw with water or malt-extract, modification of Etter's

medium, dung-extract agar, potato malt agar and potato glucose agar. Only a few of the 87 media tested were valuable for the production of fruiting-bodies.

Failure of poisons and "growth-promoting" substances to induce the formation of fruiting-bodies must mean that the production of fruiting-bodies depends upon more than the stimulus given by the substances as they were used in the experiment.

#### GENETICAL STUDIES

#### Materials and methods

The species that were used in this phase of the study are as follows: <sup>3</sup> Anellaria separata (Fries) Karsten, Coprinus fimetarius macrorhizus Fries, C. micaceus Fries, C. plicatilis Fries, C. radians Fries, C. semilantanus Peck, Naucoria semiorbicularis (Fries) Quél., Panaeolus papilionaceus (Fries) Quél., P. retirugis (Fries) Quél., Psathyrella disseminata (Fries) Quél., Psilocybe Foenisecii (Fries) Quél., and P. subviscida Peck.

The culture of *Coprinus radians* was from a fruiting-body that appeared on the campus of Northwestern University, Evanston, Illinois, in June, 1935. Monosporous cultures of certain fungi were secured from the Centraalbureau voor Schimmelcultures, Baarn, Holland: *Coprinus micaceus* from Belgium, *Panaeolus papilionaceus* from Vienna and *P. retirugis* from Paris. The other species were secured near East Lansing, Michigan.

In the pairing of the mycelia small masses of mycelium from any two cultures were placed a few millimeters apart on a potato malt agar medium in a test-tube. The resultant mycelium was examined after two to four weeks for the presence of clampconnections.

#### RESULTS OF PAIRINGS

Mycelia from the same fruiting-body

The results are given in Table 1.

"See first footnote under "Materials and methods" of culture studies.

TABLE 1

RESULTS OF PAIRINGS OF MONOSPOROUS MYCELIA OF VARIOUS AGARICS

Species	Number of monosporous mycelia used	Results
Anellaria separata	18	Regularly quadripolar
Coprinus fimetarius macrorhizus	29	Irregularly bipolar
Coprinus micaceus		No. ale con a contraction of
(culture 16a)	9	No clamp-connections
(culture 127)	19	Irregularly bipolar? or ir- regularly quadripolar?
Coprinus plicatilis	16	Regularly quadripolar. False clamps in certain combinations
C. radians	21	No clamp-connections
C. semilantanus		Regularly quadripolar
Naucoria semiorbicularis	14	regularly quadripolar
(culture 106)	17	Regularly bipolar
(culture 112)	8 15 9	Regularly bipolar
Psathyrella disseminata	15	No clamp-connections
Poilouka Faminaii	10	
Psilocybe Foenisecii	45	Irregularly quadripolar
P. subviscida	17	Probably bipolar with many irregularities

## Geographic races

### COPRINUS MICACEUS

Nine mycelia of culture 127 and nine of culture 16a (both from East Lansing, Michigan) were paired. No clamp-connections were formed. This was not unexpected since culture 16a had changed (all nine mycelia) in color and spore type since it was first cultured.

Cultures from Belgium were paired with cultures 16a and 127. No clamp-connections were formed.

## NAUCORIA SEMIORBICULARIS

Eight mycelia of culture 112 were paired in all combinations with eight mycelia of culture 106. These two cultures were collected within one and one-half miles of each other. Clamp-connections were found in all but two of the pairings.

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## Interspecific pairings

The results are given in Table 2.

TABLE 2

Results of Pairings between Monosporous Mycelia of Different Species

Cross	Number of pairings	Results
Coprinus semilantanus $\times$ C. fimetarius macrorhizus C. micaceus (culture 16a) $\times$ C. fimetarius macrorhizus. C. micaceus (culture 127) $\times$ C. fimetarius macrorhizus. C. micaceus (culture 127) $\times$ C. plicatilis Panaeolus papilionaceus $\times$ P. retirugis	32 32 32	No clamps No clamps No clamps No clamps No clamps

### Intergeneric pairings

The results are given in Table 3.

TABLE 3

RESULTS OF PAIRINGS BETWEEN MONOSPOROUS MYCELIA
OF DIFFERENT GENERA

Cross	Number of pairings	Results	
Anellaria separata × Panaeolus papilionaceus	16 24	No clamps One to three clamps found in each of four pairings	
A. separata $ imes$ Panaeolus retirugis	-1 16	One clamp-like structure in one of the pairings	
N. semiorbicularis $\times$ P. papilionaceus .	16	No clamps	
N. semiorbicularis $\times$ P. retirugis	12	No clamps	
Coprinus plicatilis × Psathyrella dis- seminata	32	No clamps	

#### DISCUSSION AND CONCLUSIONS

On the basis of clamp-connections, it could not be decided whether *Coprinus radians* was homothallic or heterothallic. Brunswik (1), on the basis of the formation of fruiting-bodies, and Chow (2) and Vandendries (15, 16), on the basis of the distribution of clamps, concluded that the species is bipolar.

Also in the case of *Psathyrella disseminata* the absence of clamp-connections prevented determination of whether the species is homothallic or heterothallic. Vandendries (17), however, found,

on the basis of the distribution of clamp-connections, that the fungus was bipolar.

The results of the writer's studies indicate that the following species are bipolar: Coprinus fimetarius macrorhizus and Naucoria semiorbicularis.

The following species were found to be quadripolar: Anellaria separata, Coprinus plicatilis, C. semilantanus and Psilocybe Foenisecii.

The great number of irregularities in the formation of clamp-connections made it impossible to decide definitely whether *Coprinus micaceus* (culture 127) and *Psilocybe subviscida* were bipolar or quadripolar. The writer thinks it likely that the former was quadripolar and the latter bipolar.

Irregularities in the pairing-reaction were found in Coprinus micaceus (culture 127), C. semilantanus, Psilocybe Foenisecii and P. subviscida.

In no species was there evidence of barrage such as found by Vandendries and Brodie (19).

False clamp-connections were found only in *Coprinus plicatilis*. They developed only in those combinations that would result in a mycelium heterozygous for the factor A and its allelomorph a, and homozygous for the factor B or its allelomorph b. Such a condition was found by Quintanilha (14) in *Coprinus fimetarius*.

In regard to geographic races it was found that spores from two fruiting-bodies of *Naucoria semiorbicularis* collected about one and one-half miles apart were compatible in almost all combinations. In *Coprinus micaceus* no clamp-connections formed in any of the combinations of mycelia from near East Lansing, Michigan, or in the combinations of mycelia from that city with mycelia from Belgium.

No interspecific crosses were obtained. Vandendries (15, 18) has obtained a few interspecific crosses.

Of the six intergeneric crosses that were attempted, clamp-connections were found very infrequently in one-sixth of the pairings of Anellaria separata with Naucoria semiorbicularis. In one of the pairings of A. separata with Panaeolus retirugis a structure that somewhat resembled a clamp-connection was found. In the other four sets of pairings of different genera no clamps were found.

The author has not found in the literature any record of an intergeneric cross in the Agaricaceae.

It seems advisable to point out that in all of the work dealing with the production of clamp-connections between different species and genera in the agarics only a small number of spores have been used. It seems to the author quite possible that many more crosses could be obtained if the workers were to use large numbers of monosporous mycelia in the pairings.

Apparently almost everyone has explained the irregularities of the pairing-reaction and the existence of geographic races as due to the mutations of the genes that influence the diploidization of mycelia. Such an explanation *may* be the best one, but the author thinks that perhaps too much emphasis has been placed upon the idea of mutations. Dickson (3) has suggested that the formation of abnormal sporophores of *Coprinus sphaerosporus* might be due to the presence in at least one of the mycelia of a number of recessive genes and/or such chromosome aberrations as translocations and deletions. Perhaps such a condition would explain other results obtained in the study of agarics.

#### ACKNOWLEDGMENT

The writer is deeply grateful to Dr. E. A. Bessey for his encouragement, advice and assistance during this study.

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# A NEW SPECIES OF DOTHIORA ON ASPEN AND WILLOW

C. L. Shear and Ross W. Davidson (WITH 3 FIGURES)

Several species of the genus *Dothiora* Fries are common and widely distributed, but detailed studies of their conidial stages have not been reported. The present paper describes a new species of this genus and includes the results of a study of its conidial stages in pure culture. The cultures were also compared with ascospore cultures of *Dothiora Sorbi* (Wahl.) Fuckel.

## Dothiora polyspora Shear & Davidson, sp. nov.

Ascocarps innate-erumpent, depressed-pulvinate, circular or irregular in outline, densely gregarious, smooth, black; locules single or occasionally several, thick lenticular, astomous (Fig. 1, A, B); asci polysporous (24 or more spores), cylindric-clavate, short stipitate,  $90-115 \times 12-15 \mu$ , aparaphysate; spores when mature muriform with 3 transverse septa and frequently 1 or rarely 2 longitudinal septa in the upper cells, clavate, constricted in the middle, upper half broader, hyaline,  $15-18 \times 5-6 \mu$ . Conidia in culture hyaline, 1-celled,  $8-15 \times 4-6 \mu$  in size, borne on the mycelium as in *Dematium*; pycnidia in culture on sterilized willow twigs resemble those of the genus *Dothichiza* Lib., producing hyaline, 1-celled spores,  $6-10 \times 3-5 \mu$  in size.

Ascomatibus dense aggregatis, innato-erumpentibus, pulvinatis, levibus nigris; loculis monostichis, intus pallidis, astomis; ascis tereti-clavatis, breve stipitatis, aparaphysatis, polysporis,  $90-115 \times 12-15 \,\mu$ ; sporidiis hyalinis, muriformibus, 3 septatis, medio constrictis,  $15-18 \times 5-6 \,\mu$ .

Hab.: Branches of *Populus tremuloides aurea* (Tidestrom) Daniels and *Salix* spp., Mesa Lakes, Grand Mesa Mt., Colo., 9800 ft. elev., coll. R. W. Davidson June 18, 1930 and June 1, 1938. Type no. 4222 (F. P. 71991), on *Populus tremuloides aurea*, deposited in the Mycological collections of the Bureau of Plant Industry.

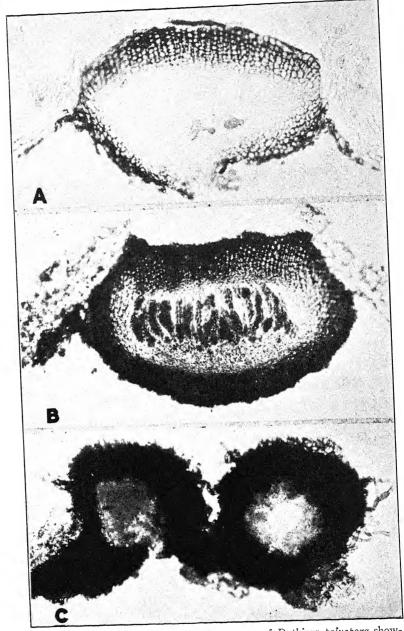


Fig. 1. A and B, sections through ascocarps of  $Dothiora\ polyspora\ showing structure. <math>A$ , immature ascocarp; B, mature ascocarp; C, section through pycnidia of D.  $polyspora\ developed$  in culture on sterilized willow twigs.

Dothiora polyspora differs from D. sphaeroides (Pers.) Fries (3) and D. Salicis Vleugel (6), the two species already described on Populus and Salix, in its polysporous asci and smaller ascospores. It is, of course, possible that D. polyspora is a polysporous form or variety of D. Salicis, as the spores average approximately one-half the size of those in that species. The number of spores, however, is consistently greater than 16 in all the material collected in 1930 and 1938 with the normal number probably being 32. Heretofore species with polysporous asci have generally been placed in separate genera, but unless there are other distinct differences we do not think they should be separated. As already suggested polysporous forms may be only varieties of common 8-spored species.

## HOST RELATIONSHIP

The presence of *Dothiora polyspora* on dead tips of living twigs of aspen and willow and on stem cankers of young aspen (FIG. 2, A–D) suggests that it may be a weak parasite, but a test of its parasitism by inoculation with pure cultures has not been attempted. Since it was collected only at a high elevation it seems possible that frost injury may predispose the hosts to infection. The stem cankers were typically annual.

Most of the specimens were collected on an open rocky area near Sunset Lake at the Mesa Lakes resort. Snow was still several feet deep in places on the area and the leaf buds had not begun to open on June 1. Most of the aspen was small and scrubby and apparently received little protection from larger trees.

## CONIDIAL STAGES IN CULTURE

Ascospores of *Dothiora polyspora* placed on agar medium (Difco-corn-meal agar, at 11° C.) swelled noticeably during the first 24 hours and some of the swollen cells had germinated (FIG. 3, A, B). Single asci containing mature spores had numerous germ tubes growing out through the ascus wall. Growth thereafter continued very slowly, but hyaline 1-celled conidia which had apparently budded off of the young hyphae were present in the cultures at the end of the second day (FIG. 3, C). Except for the extremely slow growth, about 15 mm. in diameter in 2 weeks, the

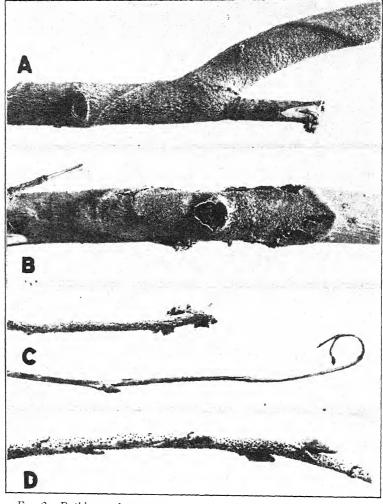


Fig. 2. Dothiora polyspora on aspen and willow. All show the densely aggregated fruiting pustules. A and B, cankers on aspen stems; C, fruiting on dead tips of aspen twigs; D, same on willow twig. Photographs by M. L. F. Foubert.

cultures were similar to cultures of fungi belonging to the form genus *Dematium*. On corn-meal or malt agar the hyphae are mostly short, crooked and multi-septate, being composed largely of swollen, somewhat rounded, light to dark brown cells. The conidia bud off from the irregular hyphal cells and are variable in size

from  $8-15 \times 4-6 \,\mu$ . Ascospores incubated at a room temperature of about 28° C. failed to grow.

Single-ascospore cultures of *Dothiora polyspora* were compared with single-ascospore cultures of *Dothiora Sorbi*, an 8-spored species, and it was found that their conidial stages were very similar. The ascospores of D. Sorbi swell greatly during the first day and continue to enlarge mostly by cell division, rather than by elongation of germ tubes, during the second and third days (FIG. 3, E, F). Only a few short hyphae were seen at the margin of the rounded, mound-like, cellular mass. Hyaline conidia budded off from these mound-like growths during the second day of incubation (FIG. 3, G). Later the cultures became dark and developed more nearly normal hyphae. Brefeld (1) recorded similar observations for D. Sorbi ascospores, but he obtained no mycelial development as he did with Sphaerulina intermixta (Berk. & Br.) Sacc. and Dothidea (?) polyspora Brefeld, two other species with Dematium-like conidial stages, which he studied in culture.

Steam-sterilized willow twigs were inoculated with single-ascospore cultures of *Dothiora polyspora*. Some of them were incubated in a refrigerator at 11° C., and others were incubated at a temperature of about 25° C. for a period of several months. Some of the twigs held at 25° C. developed small globular pycnidia on their surface and from these hyaline 1-celled spores (6–10  $\times$  3–5  $\mu$  in size) were extruded in long, delicate, ribbon-like, white cirrhi. Twigs held at 11° C. developed numerous similar small globular masses but none was found to contain spores.

Sections through the pycnidia developed on the willow twigs disclosed an irregular cavity containing numerous 1-celled, hyaline spores but no conidiophores. The walls were thick, irregular, and with no definite structural arrangement (Fig. 1, C). No ostioles were seen. In structure and development the pycnidia in pure culture were more nearly like those of the form genus *Dothichiza* Lib. (4). Macroscopically the pycnidia appeared to have developed on the surface of the twigs, but sections showed them to be erumpent through the outer bark.

## PYCNIDIA IN NATURE

Several pycnidial forms were present on some of the willow twigs on which *Dothiora* was fruiting, but none of these was definitely proved to be the pycnidial stage of *D. polyspora*. The pycnidial stage which is thought to be a form of this ascomycete was previously referred to *Dothichiza* sp. (2). The host relationship of this *Dothichiza* and its macroscopic appearance, especially its dense aggregation of pycnidia on dying tips of twigs, are similar to those of *Dothiora polyspora* (Fig. 2, *D*). The pycnidia are erumpent through the epidermis. At first the stroma is delicate

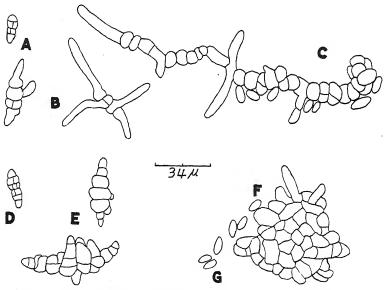


Fig. 3. A-C, Dothiora polyspora. A, ascospore; B, germinating ascospores after one day on corn-meal agar; C, two-day growth, showing conidia around hypha. D-G, Dothiora Sorbi. D, ascospore; E, germinating ascospores after one day on corn-meal agar; F, germinating ascospore after two-day development; G, conidia.

and inconspicuous with the conidia developing just underneath the epidermis on a somewhat heavier basal aggregate of fungus tissue, which apparently gradually develops into a heavier dark sclerotoid mass of fungus cells. This heavy stroma-like structure appears to be an ascocarpic primordium.

This Dothichiza form collected on willow twigs at Grand Mesa in 1930 is somewhat similar to D. tremulae (Sacc.) Hoehn., which was first described by Saccardo (5) as Phoma tremulae, but it is not the same species. It is interesting to note that von Hoehnel referred P. tremulae to Dothichiza (4) and implied that it is most certainly a stage of Dothiora. If, as von Hoehnel suggested, species of Dothichiza of this type are usually imperfect stages of Dothiora it is reasonable to expect the Dothichiza sp. from Colorado to be an imperfect stage of Dothiora polyspora.

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# THREE PEZICULA SPECIES OCCURRING ON ALNUS<sup>1</sup>

J. Walton Groves <sup>2</sup>
(with 12 figures)

The occurrence of species of the genus *Pesicula* on *Alnus* appears to have almost entirely escaped notice in North American literature with the exception of *Dermatea Alni* Rehm, reported by Povah (1935) from Michigan. Early records of *Patellaria rhabarbarina* Berk, on this host by Curtis (1867) and Peck (1869) are probably based on a *Pesicula*, but no description was given. The true *P. rhabarbarina* is a *Pesicula* occurring on *Rosa* and it is improbable that the fungi collected on *Alnus* belonged to this species.

In the Temagami Forest Reserve, Ontario, three well-defined species of *Pezicula* occur on this host. In this region two species of *Alnus* are found, *A. incana* (L.) Moench. and *A. crispa* var. *mollis* Fernald, and the fungi show a certain amount of host specialization. *Pezicula aurantiaca* Rehm has been collected only on *A. crispa* var. *mollis*, *P. Alni* Rehm chiefly on *A. crispa* var. *mollis*, but occasionally on *A. incana*, and the third species, which appears to be undescribed, has been found only on *A. incana* with one collection on *Betula lutea*.

These three species were cultured from both ascospores and conidia and the cultures were grown on two per cent malt extract agar and on sterilized twigs of the host. The twig cultures were prepared as described in an earlier paper (Groves 1936). The cultures from ascospores and conidia were similar and both re-

<sup>&</sup>lt;sup>1</sup> Contribution No. 596 from the Division of Botany and Plant Pathology, Science Service, Department of Agriculture, Ottawa, Canada. Part of the work was done at the Department of Botany, University of Toronto, and was included in a thesis presented to the School of Graduate Studies of that University in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

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turned the same type of conidial stage in culture but no apothecia were developed. The appearance of the cultures of each of the three species was distinctive, and each could readily be distinguished by means of the conidia. The following descriptions are based on the material used in these studies.

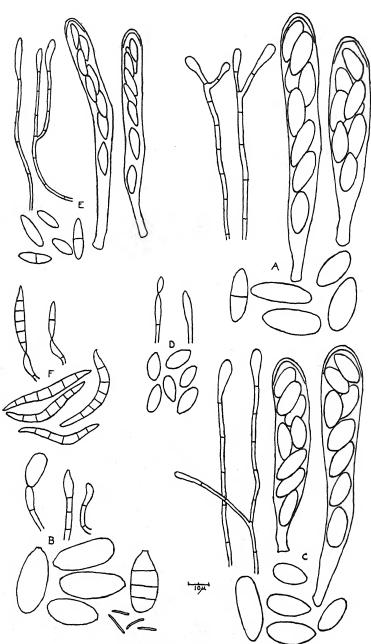
Pezicula aurantiaca Rehm, Ber. Bayer. Bot. Ges. 13: 198. 1912.

Habrostictis aurantiaca Rehm, 26 Ber. Nat. Ver. Augsburg 26: 67. 1881.

Ocellaria aurantiaca Rehm, Rab. Krypt.-Fl. 13: 135. 1889.

Apothecia erumpent to subimmersed, scattered, separate, occasionally two or three in a cluster, circular or somewhat irregular, sessile, scarcely narrowed below, 1–2 mm. in diameter, 0.3–0.5 mm. in height, waxy in consistency, more fleshy when moist; hymenium concave to plane or slightly convex, slightly pruinose, "buffy brown," "light brownish olive," "tawny olive," much brighter when moist, close to "ochraceous orange," sometimes deciduous, margin at first thick, brighter than hymenium and conspicuous, later sometimes disappearing; tissue of the hypothecium compact, pseudoparenchymatous, composed of hyaline or pale-yellowish almost isodiametric to more or less elongated cells about 5-12  $\mu$  in diameter, and with the walls grown together, arranged in more or less vertically parallel rows, curving obliquely toward the outside; subhymenium a narrow zone composed of slender, interwoven hyphae; asci cylindric-clavate, short-stalked, 8-spored, (80)-100- $125-(140) \times 15-20 \mu$ ; ascospores oblong-ellipsoid to ovoid, hyaline, straight or sometimes slightly curved, one celled, occasionally 2-4 celled, irregularly biseriate to crowded,  $18-32 \times 8-12 \mu$ ; paraphyses hyaline, filiform, septate, simple or branched,  $1.5-2.0 \mu$  in diameter, widened at the tips to about  $5 \mu$  and forming a slight epithecium.

The conidial fruiting bodies are inconspicuous, developing beneath the outer bark layers and raising and splitting them, but scarcely breaking through, the spores emerging through the cracks in the bark in whitish masses. The stromata are circular to slightly elongated, 0.4–1.2 mm. in diameter, obtusely conical to cushion-shaped or discoid, up to 0.5 mm. in thickness in the central part, waxy when dry, more fleshy when moist; the tissue composed of closely interwoven, ascending hyphae, about 3–5  $\mu$  in diameter, forming a more or less indefinite but slightly more compact zone below the fruiting surface; conidiophores borne more or less ex-



Figs. 1-3.

posed over the upper surface or in widely opening cavities, hyaline, cylindric to sub-clavate, simple, occasionally branched, continuous or septate, very variable in length,  $15-25-(65) \times 3-5 \mu$ , and sometimes swollen below the point of attachment of the spore up to  $7 \mu$ ; conidia oblong-ellipsoid, to ovoid, hyaline, one-celled, occasionally 2-4-celled, straight or slightly curved, ends rounded, one end with a truncate apiculus,  $25-40 \times 12-16 \mu$ ; microconidia not observed in nature but in culture are hyaline, filiform, straight or curved, one-celled,  $6-14 \times 1.5-2.0 \mu$ .

Host: Alnus crispa var. mollis Fernald.

Type: Rehm: Ascomyceten 266.

Exsiccati: Rehm: Ascomyceten 266.

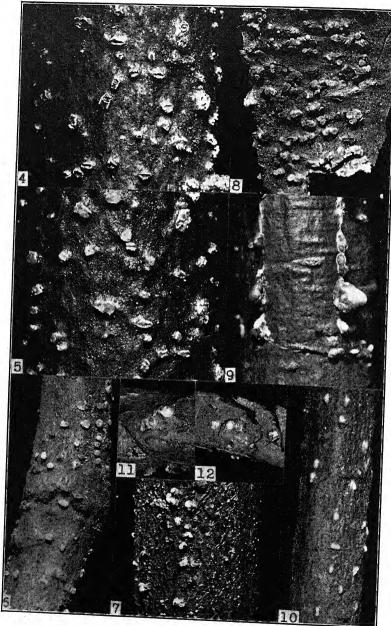
Specimens examined: University of Toronto Herbarium. On Alnus crispa var. mollis. 8434 (407), 8405 (426), Temagami Forest Reserve, Ontario. Durand Herbarium. 7519. A fragment of Rehm: Ascomyceten 266. Herbarium of J. W. Groves. On Alnus crispa var. mollis. 418, 483, Temagami Forest Reserve, Ontario.

On malt extract agar the colonies reach a diameter of about 4 cm. in three weeks. They are whitish at the margin, becoming more or less zoned and variously coloured toward the centre, "sea foam green," "sea foam yellow," "honey yellow," to "yellowish citrine," with downy to velvety aerial mycelium, sometimes with white, cottony tufts. The tissue is composed of interwoven hyphae as in nature, but is looser, and the walls of the hyphae are more distinct. The conidia are produced in irregularly lobed cavities which tear open widely, exposing the whitish spore masses. The conidia and conidiophores are typical and microconidia are present.

On twigs of Alnus crispa var. mollis and A. incana this species grows equally well in culture. Usually a whitish to buff or brownish, cottony tuft of aerial mycelium develops at the point of inoculation, but does not spread over the twig. The conidial stromata

<sup>3</sup> The numbers in brackets refer to duplicate specimens in J. W. Groves' herbarium.

Figs. 1-3. 1, *Pezicula aurantiaca*, A, asci, ascospores, and paraphyses, B, conidiophores, conidia and microconidia; 2, P. Alni, C, asci, ascospores, and paraphyses, D, conidiophores and conidia; 3, P. alnicola, E, asci, ascospores, and paraphyses, F, conidiophores and conidia.



Figs. 4-12.

are erumpent, breaking through the bark and developing on the surface, usually separate, scattered, downy to tomentose, whitish to buff or cinnamon, almost globose, 0.3–2.0 mm. in diameter, containing one or more globose to irregularly lobed cavities. The tissue is sometimes pseudoparenchymatous at the base, but mostly composed of interwoven hyphae with a compact zone surrounding the cavity, and a loose weft of hyphae at the outside. The conidiophores and conidia are typical and microconidia are produced.

Pesicula aurantiaca can be readily distinguished from the other two species by its gross appearance. The apothecia are of a different colour and much larger than in the other species, and have a characteristic immersed habit of growth becoming more strongly erumpent when moist. In this respect, P. aurantiaca is similar to the common Ocellaria ocellata (Pers.) Schroet. occurring on Salix and Populus. When a series of species including O. ocellata, P. aurantiaca, and P. Corni Petr. are considered, it is found impossible to draw a clear cut generic distinction between Ocellaria and Pesicula.

The conidial fruiting bodies could be referred to the form genus *Cryptosporiopsis*. The conidia are of the typical oblong-ellipsoid form, usually found in the imperfect stages of *Pesicula* species. They can be distinguished from the conidia of *P. Alni* by their larger size and more oblong shape.

Pezicula Alni Rehm, Ber. Bayer. Bot. Ges. 13: 199. 1912.

Pezicula quercina f. Alni Fuckel, Symb. Myc. Nachtr. 2: 56.

1874.

Dermatella quercina var. Alni Sacc. Syll. Fung. 8: 490. 1889. Dermatea Alni Rehm, Rab. Krypt.-Fl. 1<sup>3</sup>: 252. 1889.

Apothecia erumpent, scattered, mostly separate, occasionally with two or three in a cluster, circular to slightly elongated, sessile,

Figs. 4-12. 4, apothecia of  $Pesicula\ aurantiaca$  in dried condition; 5, apothecia of  $P.\ aurantiaca$  moistened; 6, apothecia of  $P.\ alni$ ; 7, conidial stage of  $P.\ alni$  on a twig in culture; 8, apothecia of  $P.\ alni$ cola; 9, conidial stage of  $P.\ alni$ cola on a twig in culture; 10, conidial stage of  $P.\ aurantiaca$  in nature; 11, conidial stage of  $P.\ aurantiaca$  in nature with a portion of the outer bark removed to show the fruiting bodies; 12, conidial stage of  $P.\ alni$ cola in nature with a portion of the outer bark removed to show the fruiting bodies. All  $\times$  4 approx.

slightly narrowed below, 0.3-0.8-(1.0) mm. in diameter and 0.5 mm. or less in height, brittle, waxy in consistency, softer and more fleshy when moist; hymenium plane to convex, slightly pruinose, at first with a slightly paler margin which soon disappears, brownish-ochraceous, brighter when moist, "cinnamon buff" to "ochraceous-buff," sometimes close to "deep colonial buff," excipulum concolorous becoming darker toward base; tissue of the basal stroma compact, pseudoparenchymatous, composed of irregular cells 3-8  $\mu$  in diameter, the walls dark coloured and grown together, the hypothecium composed of more or less vertically parallel, colourless, hyphae, curving obliquely toward the outside and forming a darker, pseudoparenchymatous, excipulum two to three cells in thickness; subhymenium indefinite, asci clavate, broad, four- or eight-spored, mostly eight-spored, (85)-100-120-(130)  $\times$  (13)-15-18-(20)  $\mu$ ; ascospores oblong-ellipsoid, hyaline, straight, one-celled, occasionally 2-4-celled, irregularly biseriate, (12)-15-20-(25)  $\times$  (5)-7.5-10  $\mu$ ; paraphyses hyaline, filiform, septate, usually branched,  $2.0-2.5 \mu$  in diameter, the tips swollen up to 7-8  $\mu$ , clavate to subglobose, forming a slight epithecium.

The conidial fruiting bodies are extremely inconspicuous, developing beneath the outer bark layers and splitting them, but scarcely breaking through, the conidia emerging in whitish masses. The stroma is slightly conical to cushion-shaped or flattened, about 0.4-0.6 mm. in diameter and 0.3 mm. in thickness at the centre, blackish, waxy when dry, more fleshy when moist, the tissue similar to the basal stroma of the apothecia; conidiophores hyaline, cylindric to clavate, simple or occasionally branched, continuous or sometimes septate,  $12-30 \times 2.5-4 \mu$ , borne over the outer surface of the stroma, conidia ovoid to oblong-ellipsoid or sub-fusiform, hyaline, one-celled, one end with a small, truncate apiculus, (12)-

14–18–(20)  $\times$  5–7.5  $\mu$ . Microconidia not observed.

Host: Alnus crispa var. mollis Fernald, A. incana (L.) Moench., Alnus spp.

Type: Rehm: Ascomyceten 463.

Exsiccati: Rehm: Ascomyceten 463; Krieger, Fungi Sax. 1625.

Specimens examined: University of Toronto Herbarium. On Alnus crispa var. mollis. 6110 (159), 8406 (414), Temagami Forest Reserve, Ont. On A. incana. 8407 (417), Temagami Forest Reserve, Ont. On Alnus sp. Ex herbarium University of Michigan, F. P. 731, Isle Royale, Mich. Durand Herbarium. 6338. On Alnus sp. Rav. Fungi Car. 5: 46 (as Patellaria rhabarbarina). Farlow Herbarium. Ex. Herb. Barbey-Boissier. 1122. Coll. Fuckel. Herbarium of J. W. Groves. On Alnus crispa var. mollis 452, Temagami Forest Reserve, Ont. 496, 556, Glenmont, Nova Scotia. On Alnus sp. 515, Portapique, Colch. Co., Nova Scotia, L. E. Wehmeyer (1602).

On malt extract agar the colonies grow slowly reaching a diameter of about 2 cm. in three weeks. They have a narrow, whitish margin, shading abruptly to olive-gray, and becoming dark-gray to olivaceous-black with short, velvety-cottony, aerial mycelium, sometimes forming gray to whitish tufts. The conidial stromata are usually produced abundantly, 0.5–1.0 mm. in diameter, olive-gray to whitish, almost globose, downy-tomentose, tissue composed of rather loosely interwoven, brownish hyphae, 3–4  $\mu$  in diameter; conidiophores very variable in length, longer than in nature, septate, and much branched, intermingled with branching, hyphal threads about 1.5  $\mu$  in diameter; conidia typical.

On twigs of *Alnus* the aerial mycelium is fairly abundant, forming a whitish to olive-gray, cottony, cushion-like tuft at the point of inoculation and spreading more or less over the twig. The conidial fruiting bodies are erumpent, scattered, globose to cylindric, whitish to olive-gray, downy-tomentose, mostly 0.5–1.5 mm. in diameter and 0.5–1.0 mm. in height, containing one or more rounded or irregularly lobed cavities, and splitting open at the top or sides. The tissue is pseudoparenchymatous at the base, composed of dark, irregular cells, the cells becoming more elongated and arranged more or less vertically above, finally prosenchymatous around the cavities; conidiophores and conidia typical.

Pesicula Alni and the following species are fairly similar in gross appearance, although P. Alni is usually less caespitose, slightly darker coloured and slightly larger. In the apothecial stages they can be separated most readily by the width of the asci and spores which are both broader in P. Alni. They also differ in the tissue structure of the apothecia and in the appearance of the cultures, but the most striking difference is to be found in the conidial stages where the conidia in the one species are ovoidellipsoid and in the other are elongated to subfiliform.

There has been some slight confusion in the nomenclature of P.

Alni and it was necessary to decide to which of these fungi this name should apply. Fuckel (1874) reported a fungus on Alnus which he believed to be identical with his Pezicula quercina, but he gave no description and cited no specimen.

Rehm (1889) published a full description based on the specimen in Rehm: Ascomyceten 463 under the name Dermatea Alni (Fuckel) Rehm.

Saccardo (1889) proposed the combination *Dermatella quercina* var. *Alni* (Fuckel) Sacc., and added a short description, based also on Rehm: Ascomyceten 463.

Finally, Rehm (1912) transferred the fungus to *Pezicula*, and stated that a Fuckel specimen in Herbier Barbey-Boissier was identical. In this account he also cited the specimen in Krieger Fungi Sax. 1625.

It is evident then that for nomenclatural purposes we must disregard Fuckel's reference and consider Rehm as the author of the species and Rehm: Ascomyceten 463 as the type. The writer has examined Rehm: Ascomyceten 463, Krieger, Fungi Sax. 1625, and a Fuckel specimen in the Farlow Herbarium from Herbier Barbey-Boissier, which may be the same collection that Rehm examined. These specimens, together with the ascus and spore measurements in Rehm's description leave no doubt that his conception of *P. Alni* applies to the broad-spored species.

## Pezicula alnicola sp. nov.

Pesicula Alni Niessl. in herb.

Apotheciis erumpentibus, dispersis, caespitosis, raro solitariis, orbicularibus vel mutua pressione distortis, sessilibus, 0.2–0.5–(1.0) mm. diam., 0.5 mm. altis, in sicco ceraceis, in humido carnosis; hymenio concavo vel plano, alutaceo-cinnamomeo, leviter pruinoso, margine primum pallide dein evanescente; hypothecio prosenchymato; ascis cylindricis vel cylindraceo-clavatis, breve stipitatis, octosporis, 70– $110 \times 8$ –12– $(14) \mu$ ; ascosporis elliptico-fusiformibus, hyalinis, continuis vel triseptatis, rectis vel leviter curvatis, irregulariter biseriatis vel uniseriatis, (12)–15–20– $(25) \times 3.5$ –5.0– $(7.0) \mu$ ; paraphysibus hyalinis, filiformibus, septatis, simplicibus vel ramosis, 1.5– $2.0 \mu$  diam., apice ad  $5 \mu$  incrassatis, leve epithecium formantibus.

Apothecia erumpent, scattered, mostly in clusters of 5–10 or more, sometimes single, circular or irregular from crowding, sessile, narrowed below, 0.2–0.5–(1.0) mm. in diameter, 0.5 mm. or less in height, brittle, waxy when dry, more fleshy when

moist; hymenium concave to plane or slightly convex, "light pinkish cinnamon" to "cinnamon" or "warm buff," slightly pruinose, at first with a delicate, paler, slightly raised margin which later may disappear; tissue of the hypothecium composed of interwoven, ascending hyphae, 3-8 µ in diameter and with the walls more or less gelatinized and grown together, sometimes looser above; asci cylindric to cylindric-clavate, short stalked, eight-spored,  $70-110 \times 8-12-(14) \mu$ ; ascospores ellipsoid-fusiform, hyaline, one- to four-celled, straight or slightly curved, irregularly biseriate to uniseriate, (12)-15- $20-(25) \times 3.5-5.0-(7.0) \mu$ ; paraphyses hyaline, filiform, septate, simple or branched, about 1.5–2.0  $\mu$  in diameter, swollen at the tips up to  $5 \mu$  and forming a slight epithecium.

The conidial fruiting bodies are very small and inconspicuous, developing beneath the outer bark layers and splitting them, but scarcely breaking through, the spores emerging in whitish masses. The stromata are usually circular, about 0.3-0.6 mm. in diameter, slightly conical to cushion-shaped, up to 300 µ in thickness at the centre, composed of interwoven, ascending, hyaline to yellowish, indistinct hyphae; conidiophores borne exposed on the upper surface or in widely opening cavities, hyaline, cylindric, pointed, continuous or septate, not branched,  $10-30 \times 1.5-2.5 \mu$ ; conidia elongate-fusiform to subfiliform, hyaline, 5–7 septate, almost straight, sickle-shaped, or sigmoid, ends pointed,  $35-53 \times 4-5 \mu$ ; microconidia not observed.

Host: On twigs and branches of Alnus incana (L.) Moench. and Betula lutea Michx.

Type: University of Toronto Herbarium. 8414, Temagami Forest Reserve, Ontario. Aug. 31, 1935.

Specimens examined: University of Toronto Herbarium. On Alnus incana. 7396 (253), 7970 (318), 8414 (416), Temagami Forest Reserve, Ontario. On Betula lutea. 8400 (325), Temagami Forest Reserve, Ontario. Durand Herbarium. On Alnus glutinosa. 6879 Europe (as Pezicula Alni Niessl.). Herbarium of J. W. Groves. On Alnus incana. 117, 125, 127, Ottawa, Ontario-250, 485, Temagami Forest Reserve, Ontario-598, Camp Mercier, Laurentide National Park, Quebec.

On malt extract agar the colonies reach a diameter of 2.5-3.0 cm. in four weeks. They are almost white to various shades of gray, often with sectors of slightly different shades of colour and rates of growth, sometimes radially furrowed and concentrically zoned, the aerial mycelium short, downy to velvety. The conidial fruiting bodies develop as rounded, more or less globose to elongated, downy, grayish stromata, up to 2–3 mm. in diameter, sometimes confluent and larger, containing a large, rounded or somewhat chambered cavity, tearing open widely; tissue of the stroma composed of closely interwoven, hyaline to yellowish hyphae about 3–5  $\mu$  in diameter, at the outside growing out into loose or somewhat tufted, hyaline, slender hyphae about 1.0–1.5  $\mu$  in diameter; conidiophores and conidia typical, the conidiophores sometimes longer than in nature.

On twigs of *Alnus* scarcely any aerial mycelium is produced. The conidial fruiting bodies are erumpent, mostly about 1.0 mm. or slightly more in diameter and about 0.5 mm. in height. They break through the bark and develop mostly on the surface as rounded, circular to elongated, grayish, downy stromata; the tissue composed of closely interwoven, hyaline to yellowish, indistinct hyphae, about 3–5  $\mu$  in diameter, the walls more or less gelatinized and grown together, containing a more or less circular to slightly lobed cavity and tearing open widely. The conidiophores and conidia are typical.

It was thought at first that this species might be *Pesicula citrinella* Rehm, also described on *Alnus*, but examination of a specimen in Rehm: Ascomyceten 262,<sup>4</sup> on which the original description was based, has shown this to be a different fungus.

Pezicula alnicola is of special interest because of the unusual type of conidial stage and again illustrates the difficulty of drawing clear-cut generic lines in this group. Groves (1939) described several types of conidial stages belonging to species of the genus Pezicula and noted that although the form of the conidial fruiting body may vary considerably in this genus, the form of the conidial spore remains relatively constant and is typically oblong-ellipsoid. In the related genus Dermatea the conidia are typically elongate-

<sup>&</sup>lt;sup>4</sup> The specimen examined was the one in the Farlow Herbarium, Harvard University. At the writer's request, Mr. E. W. Mason of the Imperial Mycological Institute, compared material of *Pesicula alnicola* with the specimen of Rehm: Ascom. 262 in the Kew Herbarium and found it to be different. This assistance is gratefully acknowledged.

fusiform to sub-filiform, but an exception was noted by Groves (1938) in *Dermatea acerina* (Peck) Rehm which has apothecia like a *Dermatea*, but oblong-ellipsoid conidia. In *P. alnicola* we have a species with apothecia like a *Pezicula* but elongate-fusiform to sub-filiform conidia.

The question might be raised here, as with *D. acerina*, whether it might not be desirable to erect a new genus for *P. alnicola*, but since it can be readily referred to *Pesicula* on the basis of the colour and consistency of the apothecia and general habit of growth, it is considered preferable to place it in an established genus until the relationships within the whole group are better understood.

## ACKNOWLEDGMENTS

The writer is indebted to Professor H. S. Jackson, Department of Botany, University of Toronto, for his continued interest and constructive suggestions.

CENTRAL EXPERIMENTAL FARM OTTAWA, CANADA

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# SCLEROTINIA BIFRONS

H. H. WHETZEL

The apothecial stage of *Sclerotium bifrons* Ellis & Ev. appears not to have been reported and described heretofore, although the sclerotial stage has been known to mycologists since 1890 when Ellis distributed it as *No. 2554* in his North American Fungi. Plant pathologists and foresters know the sclerotial stage as a frequently serious leaf pathogene of *Populus tremuloides* in North America.

The first collection of the apothecial stage of this fungus known to the writer is one made by him on April 26, 1921, near McLean, N. Y. This collection was at that time deposited in the herbarium of the Department of Plant Pathology at Cornell University, No. 11514, under the name Sclerotinia bifrons (Ellis & Ev.) Whetzel. Duplicate material of this collection under this same name was deposited shortly thereafter in the mycological herbarium of the New York Botanical Garden and in that of the University of Wisconsin.

Nearly every spring since 1921, the writer or his students have collected the apothecial stage in abundance in certain localities near Ithaca, N. Y. Critical studies on the material thus available have repeatedly been made so that the writer is thoroughly familiar with the habits and morphology of this fungus in all its stages.

On July 29, 1929, Seaver and Shope <sup>1</sup> collected abundant material of the apothecial stage of a sclerotial fungus in Colorado at an elevation of 9,600 feet, in a moist ravine under trees of *Populus tremuloides*. These trees at that time showed general leaf infection and maturing sclerotia of *Sclerotium bifrons*. The collectors at once assumed that they had discovered the apothecial stage of *Sclerotium bifrons* and reported their find under the name *Sclerotinia bifrons*. This is apparently the first published use of this combination.

<sup>&</sup>lt;sup>1</sup> Seaver, F. J. & Shope, P. F. Mycologia 22: 1-8. 1930.

Seaver and Shope make the remark (p. 3-4) that "Whether infection takes place directly from the germinating ascospores has not been determined but since the sclerotia and apothecia occur at about the same time, it is likely that it does." In fact the apothecia mature and disappear long before the new crop of sclerotia appear in the lesions on the trees. Our records show that apothecia mature and discharge their spores over a period of ten days to two weeks during the time when the leaf buds of the *Populus* are bursting and the young leaves are unfolding. About Ithaca, N. Y., this is during late April or May, depending on the season. Although inoculation usually occurs while the leaves are young and developing, lesions do not appear until these leaves are nearly or quite full grown. Mature sclerotia appear after some time in these lesions. Collection dates for specimens of the sclerotial stage throughout North America range from late June to early August.

To one familiar with the apothecia of *Sclerotinia bifrons* it is at once obvious even from their very brief descriptive remarks and from their excellent photographs that the apothecia which Seaver and Shope collected are not those of *Sclerotium bifrons*. This the writer has been able to fully confirm by a critical study of excellent material of the Colorado fungus kindly given him by Dr. Seaver.

A strict application of the rules of nomenclature in this case would apparently require that the combination *Sclerotinia bifrons* be used for the fungus, the apothecial stage of which is described and figured by Seaver and Shope. Since, however, there is here clearly involved an error in identification on their part, and since the species name is already universally associated with the common sclerotial fungus on *Populus*, both common sense and sound scientific practice would seem to sanction the application of the name *Sclerotinia bifrons* to the fungus heretofore known as *Sclerotium bifrons* Ellis & Ev., giving to the fungus of Seaver and Shope another name.

The combination *Sclerotinia bifrons* Seaver and Shope has also unfortunately appeared in print in a recently published textbook.<sup>2</sup> That there may be no further confusion regarding the proper application of the name *Sclerotinia bifrons*, a brief technical descrip-

<sup>&</sup>lt;sup>2</sup> Boyce, J. S., Forest Pathology, p. 144. 1938. Hubert in his Outline of Forest Pathology, p. 215, 1931, also uses this combination but erroneously attributes it to Ellis and Everhart.

tion of the apothecial stage of *Sclerotium bifrons* Ellis & Ev. is here presented.

## Sclerotinia bifrons Whetzel, sp. nov.

Apotheciis singulis, raro duobus vel tribus, margine cujusque sclerotii, 2–10 mm. diam., ample infundibuliformibus dein patelliformibus, 'Saccardo umber' vel cinnamomeo-fuscis, in maturitate 'natal brown'; stipite robusto, 5–25 mm. longo, fere cum radiculis junctione sclerotio; ascis octosporis, 152–200  $\times$  9–12  $\mu$ . Ascosporis oblique uniseriatis, unicellulosis, ample ovideis, uno latere leviter planis, hyalinis, biguttulatis,  $11-16 \times 4-7 \mu$ .

On the ground from sclerotia dehisced from diseased leaves of *Populus tremuloides*. Type: *No. 15624*, Herb. Dept. Plant Path., Cornell University, collected by H. H. Whetzel near McLean, New York, May 23, 1927.

It seems desirable to present also at this time a name for and a more complete technical description of the Colorado fungus collected by Seaver and Shope.

## Sclerotinia confundens Whetzel, sp. nov.

Apotheciis pluribus ad multa, superficie tenuium ovalium ad rotundate concavo-convexa nigra sclerotios crescens, cupulatis, 0.5–1.5 mm. diam., siccis pallide luteolis ad alte cremea;  $^3$  stipitibus robustis, 2–3 mm. longis, basilaribus radicularis defectis; ascis octosporis,  $45–74\times4–6.5~\mu$ ; ascosporis semiseriatis, fusiformibus ellipsoideis, hyalinis,  $7–10\times2.4–3~\mu$ .

On the ground from free lying sclerotia entangled in leaf debris, under trees of *Populus tremuloides*. Type: *No. 17867*, Herb. Dept. Plant Path., Cornell University. Collected by Seaver and Shope July 29, 1929, Colorado, elevation 9,600 feet.

It will be seen from a comparison of the above descriptions of the apothecia that the two fungi are quite distinct species. The assumption by Seaver and Shope that the sclerotia of *S. confundens* were formed in the leaves of *Populus tremuloides* and were freed after several seasons by decay of the leaf tissues, is highly improbable. All sclerotia of this type, in our experience, produce their apothecia the spring following the season in which they were formed. Moreover, a critical examination of the leaf debris layers in which the sclerotia were entangled disclosed foliar remnants of some other plant along with those of *P. tremuloides* and which may represent the real suscept of *S. confundens*.

<sup>&</sup>lt;sup>3</sup> According to Seaver and Shope (p. 3) "The whole ascophore is whitish or slightly yellowish" (when fresh, presumably).

The writer has partially completed a manuscript in which will be presented a monographic treatment of *Sclerotinia bifrons*, *Sclerotinia confundens* and a number of other closely related species. This brief preliminary discussion is published thus in advance of the main paper at the urgent request of a colleague who has ready for publication the results of a rather extensive investigation of the disease caused by *Sclerotinia bifrons*.

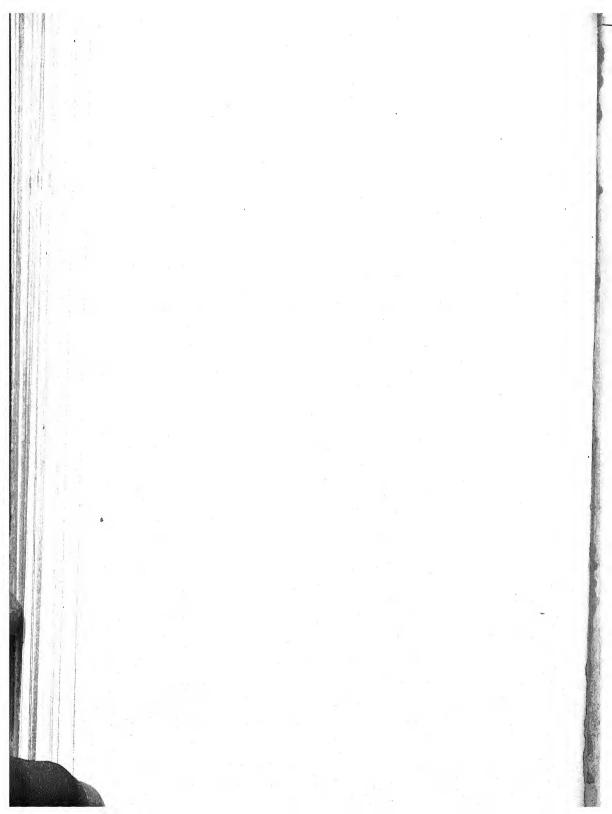
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## EDITOR'S NOTE

Two species of *Sclerotinia* have been reported on the poplar sclerotium commonly known as *Sclerotium bifrons*, one from the Rocky Mountain variety of *Populus tremuloides* (regarded by some as a distinct species, *Populus aurea* Tides.) and one from the eastern form of *Populus tremuloides*. Unfortunately the same binomial has been applied to both species of fungi. Under the International Rules of Botanical Nomenclature the later homonym is untenable and must be rejected:

Section 12. Art. 61. A name of a taxonomic group is illegitimate and must be rejected if it is a *later homonym*, that is if it duplicates a name previously and validly published for a group of the same rank based on a different type. Even if the earlier homonym is illegitimate, or is generally treated as a synonym on taxonomic grounds, the later homonym must be rejected.

Therefore, in recognition of the years of work which Professor Whetzel has spent on *Sclerotinia* in general, and the eastern species on poplar in particular, I propose that the name **Sclerotinia Whetzelii** (Syn. *Sclerotinia bifrons* Whetzel 1940. Not *Sclerotinia bifrons* Seaver & Shope 1930.) be adopted to replace the later homonym in order to avoid confusing the eastern and the Rocky Mountain species of *Sclerotinia* on poplar. A detailed account of our western species will appear at some later time.—Fred J. Seaver.



# **MYCOLOGIA**

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No. 2

# CERCOSPORA LEAFSPOT OF RED BUD

Frederick A. Wolf

(WITH 11 FIGURES)

One of the most conspicuous diseases of red bud, Cercis canadensis L., within the area comprising the Duke Forest, is a leafspot whose cause is commonly designated Cercospora cercidicola Ellis. It appears from the records of collections that this fungus is coextensive in range throughout the eastern United States with that of its host. The writer's interest in this disease has centered, for several years, in the developmental morphology of the pathogen. It has been found that the fungus possesses not only a conidial stage but also an ascigerous stage. The former may be found on living leaves throughout the entire period from April to October, and the latter matures in March on decaying leaves, beginning its development, however, during the preceding autumn, with the formation of spermatia and carpogonia.

## CONIDIAL STAGE

Cercospora leafspot can be recognized by the presence of circular to angular rusty-brown to dark-brown necrotic lesions, usually 4–5 mm. in diameter. The border is definite, raised, and dark-brown during the early part of summer, but by autumn large indefinitely limited spots having a diameter of a centimeter or more will have developed. The spots become grayish above but remain rusty-brown beneath. The tissues surrounding the necrotic areas early become yellowish-green (FIG. 11).

[Mycologia for January-February (32: 1-127) was issued February 1, 1940] The conidiophores are produced on both leaf surfaces but are much more abundant on the lower surface. They emerge through the stomates and occur for the most part in clusters of 5 to 10. They generally adhere at the base, by one-third to one-half their length, and the upper portion spreads into a loose fascicle (FIGS. 1, 2). In some cases each conidiophore of the fascicle tends to stand apart from each of the others. They are more or less branched, have prominent denticulate conidial scars, and vary in dimensions from  $50\text{--}300 \times 3\text{--}5\,\mu$ . The conidia (FIG. 4) are obclavate, straight or curved, dilutely colored, 1–3-septate, and 15–50 (mostly  $25\text{--}30\,\mu$ )  $\times$  4–6.5  $\mu$ . Conidia continue to be formed throughout the entire summer whenever moisture conditions are favorable, and meantime the stromata at the bases of the conidiophoral fascicles increase in size.

This stage of the fungus was first collected near Lexington, Kentucky, by W. A. Kellerman and was described by J. B. Ellis (1), in 1882, as Cercospora cercidicola. The organism is also included among species of Cercospora enumerated by Ellis and Everhart (3). Tehon (5), in 1924, erected the name Cercospora cercidicola var. coremioides, mainly because the conidiophores are closely adherent throughout a great part of their length. Solheim (4) expressed the opinion in his monograph that this varietal name should be relegated to synonomy since the organism is characteristically coremioid. With this opinion the present writer is entirely in accord.

## PERITHECIAL STAGE

At about the time that the leaves are being shed the lower surface of lesions may be observed to be densely occupied by dark erumpent stromata. These stromata are of two types, the spermogonial initials and the perithecial primordia, structures that can be distinguished if infected tissues are appropriately fixed, sectioned and stained. Both are spherical with a diameter ranging from 50 to  $80 \,\mu$ . As they continue development the parietal portion of each, consisting of several layers of brown, thick-walled cells, becomes differentiated. The spermogonia eventually become pycnidium-like, the interior coming to be filled with bacilliform spermatia (FIG. 6). These spermatia are embedded in a gelatinous matrix

that arises from the disintegration of the spermatiferous cells. There is evidence that spermatia are first formed near the center of the spermogonial stroma and that formation of spermatia proceeds centrifugally. As soon as the wall of the perithecial pri-

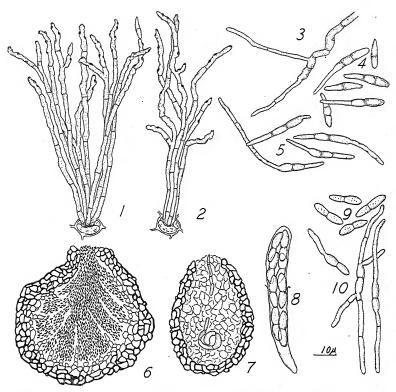


Fig. 1, loose fascicle of conidiophores of *Cercospora cercidicola*; 2, coremoid fascicle of conidiophores; 3, germinating conidiophore; 4, conidia; 5, germinating conidia; 6, mature spermagonium in vertical section; 7, perithecial primordium, in section, containing coiled archicarp with trichogne extending to the surface of the leaf; 8, ascus of *Mycosphaerella cercidicola* whose outer membrane is ruptured, and the inner membrane is extended preparatory to ascospore ejection; 9, mature ascospores; 10, germinating ascospores.

mordia has differentiated the interior will be found to be filled with cells having a deeply staining content. Moreover within each is a single coiled archicarpic apparatus whose trichogynal portion projects to the surface (FIG. 7). Although spermatiation was not

observed, it undoubtedly is accomplished with films of moisture serving as the medium of transfer of spermatia. Then by late March or early April of the succeeding spring the perithecial primordia will have become transformed into mature perithecia.

The perithecia are densely aggregated within the areas occupied by lesions during the previous year. They are completely embedded, except for the ostiolar orifices, within the leaf tissues. Nearly all open to the lower leaf surface. They range in diameter from 65–95  $\mu$ . The asci adhere in a fascicle when the perithecia are crushed in a drop of water. They measure  $35-45 \times 7-8 \mu$ . Their outer wall ruptures and the asci become elongated preparatory to discharge of the ascospores (FIG. 8). The ascospores are unequally two-celled, constricted at the septum, slightly curved, and measure  $15-18 \times 4-5 \mu$  (FIG. 9). Paraphyses are absent. These morphological features are clearly those that characterize the genus Mycosphaerella.

Apparently two species of Mycosphaerella (Sphaerella) are known to occur on Cercis, S. Cercidis Pass., and S. cercidicola Ellis & Kellerm. The former was described from Italy, occurring there on Cercis japonica Sieb., and is not known to occur in North America. The latter was first collected in Kansas in June, 1884, by W. A. Kellerman, who sent specimens to Ellis. Later in the year Ellis and Kellerman (3) described it as S. cercidicola, but their description was not included in Saccardo's Sylloge Fungorum. The writer has examined their type specimens, No. 550, deposited in the New York Botanical Garden and found them to be specifically identical with the fungus herein under consideration. Two discrepancies appear in connection with Ellis and Kellerman's (3) description. In the first place the perithecia are said to be mostly epiphyllous whereas they are found to be mostly hypophyllous. Secondly the ascospores are recorded as measuring  $11-13 \times 2.5$ 3.0  $\mu$ , but are 15–18 imes 4–5  $\mu$ . The writer's measurements were made of freshly discharged ascospores, while Ellis and Kellerman probably made measurements from dried specimens collected a few months previously. Furthermore the ascospores of certain species of Mycosphaerella are known to enlarge considerably immediately

<sup>&</sup>lt;sup>1</sup> Thanks are due Dr. F. J. Seaver, New York Botanical Garden, for courtesies in connection with my examination of specimens in the Herbarium.

prior to discharge, and the asci from dried specimens of such species never contain mature ascospores.

## GROWTH IN CULTURE

The fungus has been isolated in pure culture from conidia and from ascospores. The cultures originating from conidia were obtained by making a suspension of conidia and streaking loopfuls of the suspension over the surface of Petri dishes containing hardened potato nutrient agar. The cultures from ascospores were obtained by permitting the ascospores to be forcibly ejected onto the surface of poured agar plates. To do this, leaves bearing mature perithecia were placed in the tops of Petri dishes and the agar in the bottoms were inverted above the perithecia.

The appearance of germinating conidia (FIG. 5) and of ascospores (FIG. 10) in the early stages of colony formation resembled that of various other species of *Cercospora* and *Mycosphaerella* which the writer has studied in culture. Growth is slow, three or four months being required to produce a colony one cm. in diameter. The colonies are white to pale-brown in color, occasional ones being olivaceous-black. They are compact, elevated, almost hemispherical, and the surface is cerebroid. It is impossible at any time to distinguish cultures originating from ascospores from those originating from conidia.

The conidiophores of this fungus germinate, forming hyphae (FIG. 3), under conditions favorable for the growth of conidia. Although hyphal formation by conidiophores may be anticipated to occur, it is not a common phenomenon among the Fungi Imperfecti.

## PATHOGENICITY

Since the pure cultures remained sterile, the tests for pathogenicity were limited to the use of crude inoculum. Conidial suspensions, made by washing lesions, were applied to healthy foliage with the result that characteristic leafspots appeared two to three weeks after inoculation. When decaying leaves, bearing perithecia, were attached to healthy leaves, similar leafspots developed within three weeks. The lesions resulting from each kind of inoculum, bore conidiophores and conidia typical of *Cercospora cercidicola*. There appears to be no doubt from the infection experiments that

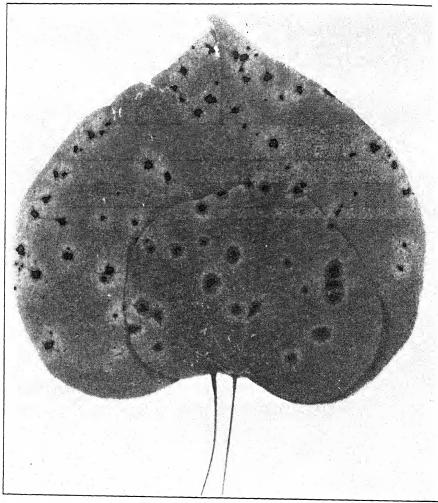


Fig. 11. Red bud leaf bearing lesions produced by action of the pathogen,  $M.\ cercidicola.$ 

the fungus is pathogenic, and that the conidial and perithecial stages are genetically connected.

## TAXONOMY

The following brief description of the red bud pathogen has been prepared since this study connects, for the first time, the conidial stage and the hibernating or perithecial stage, and since the fungus has previously not been correctly and adequately described.

Mycosphaerella cercidicola (Ellis & Kellerm.) comb. nov. emend.

Perithecia in vernale in foliis putrescentibus efformantia, vulgo hypophylla interdum epiphylla, in maculis dense dispersa, punctiformia, nigra, erumpentimmersa, sphaeroidea, 65–95  $\mu$  diam.; ascis sacciformibus, fasciculatis, aparaphysatis, octosporis, 35–45  $\times$  7–8  $\mu$ ; sporidiis sub-biseriatis, loculis inaequalis, loculo superiore crassiore constrictis, rectis vel curvulis, 15–18  $\times$  4–5  $\mu$ .

Spermogoniis et carpogoniis autumno efformantibus, innatis, paginis inferioribus in maculis exaridis occupantibus, globosis, nigris,  $50-80 \mu$ ; spermatiis bacillaribus, hyalinis,  $2-3 \times 1 \mu$ . Hab. in foliis maturissimis vel dejectis Cercidis.

Status conidicus: Statum conidicum Cercospora cercidicola Ellis sistit. Maculis initio minutis, dein expansis 3–4 mm., subcircularibus v. augulosis, denique 1 cm., subnigricantibus, denique supra griseo-albidis, infra vero rubiginosis, linea nigro-brunnea subelevata circumicirca rufo-zonata cinctis; hyphis amphiginis, laxe fasciculatis, brunneis,  $50-300 \times 3-5 \mu$ , geniculatis; conidiis oblongo-clavatis, tenuiter 3-septatis,  $13-50 \times 4-6.5 \mu$ .

Hab. in foliis vivis Cercidis canadensis L., C. Japonicae Sieb., C. occidentalis Torr.

Syn. Sphaerella cercidicola Ellis & Kellerm., Bull. Torrey Club 11: 123. 1884.

Cercospora cercidicola Ellis, Am. Nat. 16: 810. 1882. Cercospora cercidicola var. coremioides Tehon, Mycologia 16: 140. 1924.

Specimens of both the conidial and ascigerous stages have been deposited in the Farlow Herbarium, Harvard University, the Mycological Collections, U. S. Department of Agriculture, and the herbarium of the New York Botanical Garden.

#### SUMMARY

The developmental cycle of the fungus generally known as *Cercospora cercidicola* Ellis, causing a leafspot of red bud, has been studied. As a result it has been found that, in addition to the conidial stage, the pathogen possesses a perithecial stage. This perithecial stages proves to be *Mycosphaerella cercidicola* (Ellis & Kellerm.) Wolf.

The conidial stage is parasitic.

The spermogonia and carpogonia, that initiate the perithecia, are developed in late summer and early autumn.

The perithecial stage matures on decaying leaves in the following spring.

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# DASYSCYPHAE ON CONIFERS IN NORTH AMERICA. IV. TWO NEW SPECIES ON DOUGLAS FIR FROM THE PACIFIC COAST

GLENN GARDNER HAHN
(WITH 2 FIGURES)

## INTRODUCTION

As part of the investigation of the European larch-canker parasite, Dasyscypha Willkommii (Hart.) Rehm (2, 5, 6), introduced from Great Britain into Massachusetts, Dasyscyphae on native and planted Douglas fir [Pseudotsuga taxifolia (La M.) Britt.] in North America had to be distinguished. This taxonomic research was necessary because Douglas fir in Europe had been reported attacked by the larch-canker organism (5, p. 900), and Douglas fir in New England was affected by a canker (5, fig. 4) with which a Dasyscypha was associated. It thus became important to determine the relationship of the Dasyscyphae occurring on this economically important conifer. Two species on Douglas fir, the introduced European saprophyte, D. calycina Fuckel (nec Pesisa calycina Schum.) (2), and the native organism, D. Ellisiana (Rehm) Sacc. (3), a species associated with a resinous canker of planted blue Douglas fir along the Atlantic Seaboard (3; 5, pp. 903-904), have already been reported. This paper is concerned with two hitherto undescribed Dasyscypha species restricted in their habitat as far as known to Douglas fir growing on the Pacific Coast.

## TWO NEW DASYSCYPHAE ON DOUGLAS FIR

In 1930 members of the Division of Forest Pathology discovered a conspicuous open canker (FIG. 1:1) associated with a species of *Dasyscypha* on saplings and poles of Douglas fir, suppressed or growing on poor sites, in certain areas in the West. The type of canker upon which the undescribed *Dasyscypha* (1, p. 263) was

growing is somewhat similar to that produced on larch by *Dasyscypha Willkommii* (2, 5). At approximately the same time a saprophytic *Dasyscypha* also was collected on small twigs of Douglas fir in the Pacific Northwest. The western Dasyscyphae are herein described as new species.

# Dasyscypha Pseudotsugae sp. nov.

Apothecia, waxy, fleshy, sparse, scattered or closely grouped (FIG. 1:2), erumpent, at first globular, closed, opening in a roundish form, margin incurved, urn-like, becoming widely expanded, disc-like under moist conditions, when dry laterally compressed and closed, shortly but distinctly stipitate, externally whitish; disc light orange-yellow 1 to orange, 1.0-3.5 mm. diam.; excipular hairs persistent, minutely roughened, hyaline, thin-walled, cylindrical with obtusely rounded extremities, septate, cells short, 3.0-3.5  $\mu$ broad. Asci clavate, apex obtusely rounded, range (50) 47.0- $60.0 \times 3.4-5.4 \,\mu$ . Ascospores eight, uniseriate, arranged in a regular oblique manner, hyaline, smooth, continuous both in the ascus and upon germination, elliptical or elliptic-fusiform with obtuse extremities, range (100)  $3.8-7.2 \times 1.8-3.6 \mu$ . Paraphyses outranking asci, filiform, of even diameter, septate, not swollen or only slightly so toward the tip with obtuse extremities, minutely guttulate.

Conidial stage (FIG. 1:4) consisting of waxy, fleshy, erumpent, light-buff stromata, with irregular labyrinthiform cavities in which the conidia are borne, and from which they exude in an opaque droplet or tendril; conidia abstricted from the tips of short, slender, subulate conidiophores, extremities acute, simple or verticilately branched; conidia hyaline, continuous, elliptic, extremities obtuse, range (50)  $3.4-4.0 \times 2.4-3.0 \mu$ , conidia artificially produced on malt agar, range (50)  $2.4-4.0 \times 1.8-3.0 \mu$ . Germination observed.

Ascomatibus sparsis, solitariis vel gregariis, initio subglobosis, dein cyathiformibus, cupulis humidulis planiusculis, margine in sicco semper connivente, breviter stipitatis, extus albidis, tomentosis; disco luteo-aurantiaco vel aurantiaco, 1.0–3.5 mm. diam.; pilis, brevibus, hyalinis, septatis, minute asperatis, 3.0–3.5  $\mu$  crassis. Ascis octosporis, clavatis, subcylindraceis (50) 47.0–60.0  $\times$  3.4–5.4  $\mu$ . Ascosporis monostichis, continuis, hyalinis, ellipsoideis vel ellipsoideo-fusiformis, apice obtusis, (100) 3.8–7.2  $\times$  1.8–3.4  $\mu$ . Paraphysibus filiformibus, septatis, ascos superantibus, apice obtusis non vel leniter sursum incrassatulis, guttulatis.

Fructificationibus conidicis luteis, carnosis, ceraceis, erumpentibus, loculiis

<sup>&</sup>lt;sup>1</sup> The color nomenclature used is that of R. Ridgway, Color standards and color nomenclature. 1922. Washington, D. C.

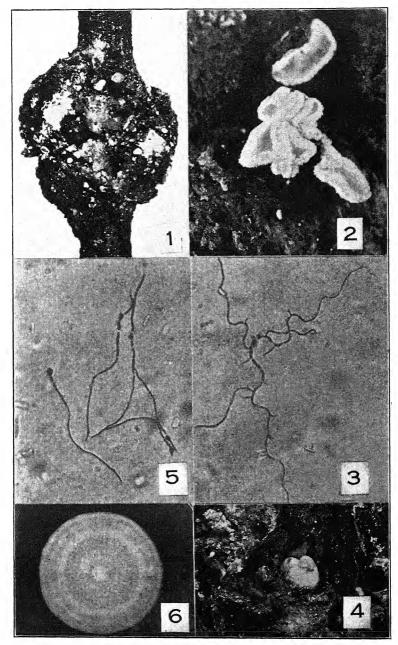


Fig. 1. Dasyscypha Pseudotsugae.

labyrinthiformibus; conidiophoris brevibus, hyalinis, filiformibus, simplicibus vel verticillate ramosis; conidiis hyalinis, continuis, ellipsoideis,  $3.4-4.0 \times 2.4-3.0 \mu$  crassis.

Hab, in ramulorum et truncorum viventium partibus aegrotis *Pseudotsugae taxifoliae* in *America Boreali*. Specimen typicum *68168*, *P. taxifolia*, in Mycological Collections, Bureau Plant Industry, U. S. D. A., Washington, D. C.

Habit. The type specimen growing on cankers collected from living branches of *Pseudotsuga taxifolia*, Lokoya, Napa County, California, by J. L. Mielke, *68168*, has been deposited in the Mycological Collections, Bureau Plant Industry.

Other specimens of the fungus collected on living branches and trunks of *P. taxifolia* from 1930 to 1939 and deposited in the collections of the Division of Forest Pathology have been studied.

California. 53062, near Hayfork, Trinity County, coll. J. S. Boyce; 53063, near Arcadia, Napa Co., J. S. B.; 53066, Alder Springs, Glenn County, coll. J. S. B.; 53084, Lokoya, Napa Co., coll. J. S. B.; 53103-4-5, Lokoya, coll. W. W. Wagener and G. G. Hahn; 64014, Dry Creek Road, Napa Co., coll. J. S. B.; 64016, Triniti, Sonoma Co., coll. J. S. B.; 64017, Hutchinson Ranch south of Santa Rosa, Sonoma Co., coll. J. S. B.; 64018, Coit Estate, near Larkmead, Napa Co., coll. J. S. B.; 68169, Siskiyou National Forest, coll. J. L. Mielke; 68170, Lokoya, coll. J. L. M.

Oregon. 40538, near Maryland College, Oswego, coll. J. R. Hansbrough; 40547, near Oakridge, coll. H. G. Lachmund and J. S. B.; 40591–92, near Zig Zag Ranger Station, Mt. Hood Nat. For., coll. J. R. H.; 40593–95–96, Zig Zag Ranger Sta., coll. T. W. Childs, J. L. M. and J. R. H.; 40597, near Kingston, coll. J. L. M. and T. W. Childs; 40599–600, near Falls City, coll. T. W. C.; 40672, Logie Trail near Portland, coll. T. W. C. and J. R. H.; 40680, Wolf Creek near Rosebery, coll. L. N. Goodding; 64015, Wolf Creek, Josephine Co., coll. J. S. B.

British Columbia. 40500, D'Arcy, near Anderson Lake Lodge, coll. J. R. H.

Dasyscypha Pseudotsugae is most closely related to D. calyciformis (Willd.) Rehm, but differs from the European species, which occurs principally on Abies, but also on Pinus, Picea, and

<sup>2</sup> Unless otherwise indicated, collection numbers denote specimens for study filed in the Division of Forest Pathology, New Haven, Conn.

Larix, in its host relationship and spore characters. D. calyciformis is most commonly found as a saprophyte but in some cases it is associated with canker formations, and accordingly has been regarded as being parasitic. The imperfect stage of D. calyciformis is nonconspicuous and its conidia germinate with great difficulty (7, pp. 15–19). On the other hand the conidia of D. Pseudotsugae occur abundantly and are readily germinable.

A pathological investigation has not been undertaken to determine whether the pronounced cankers on living trees commonly associated with Dasyscypha Pseudotsugae are caused by that fungus. Field studies on the disease have been made by different members of the Division of Forest Pathology including Boyce (1, p. 263), who discussed the canker in his text together with his observations on the disease in the known northern range of D. Pseudotsugae, as well as in its southern range. In California and Oregon the canker is commonly found on the main trunks and branches of small saplings. In the north the fungus occurs also on roughened bark, particularly about pruning wounds, on the trunks of trees of pole size up to 8 inches in diameter.

Based on present observations, Dasyscypha Pseudotsugae and the canker associated with it appear to have little pathological importance. However it still remains to be seen how the organism may behave in the future. In a pathological investigation of the disease, we shall need to discover the role of not only the perfect stage, but also that of the imperfect stage. In this instance we have two types of spores both of which are probably capable of disseminating the canker, for, as stated above, the new species, unlike the European larch-canker organism, produces functionable conidia. No one has succeeded in growing D. Will-kommii from the spores produced by its imperfect stage. Apparently the conidia play no part in the dissemination of the European canker.

## Dasyscypha ciliata sp. nov.

Apothecia (FIG. 2: 1), waxy, fleshy, usually scattered, occasionally grouped (FIG. 2: 2), at first globular, closed, opening as a flat disc under moist conditions, laterally compressed and closed when dry, very shortly but definitely stipitate, externally whitish; disc

orange, commonly 1–2 mm. diam.; excipular hairs conspicuous, elongate, minutely roughened, hyaline, thin-walled, cylindrical with subacute extremities, brittle, readily breaking away and revealing the glabrous tissue beneath, hairs about the rim persistent, fringe-like, septate, cells short, 3  $\mu$  broad. Asci (Fig. 2: 3), clavate, apex obtusely rounded, range (150) 63.0–92.8  $\times$  6.0–12.0  $\mu$ , commonly 70–80  $\times$  7–10  $\mu$ . Ascospores eight, uniseriate, arranged in a regular oblique manner, hyaline, smooth, continuous in ascus and upon germination, with a prominent guttule (Fig. 2: 3), ovate or elliptic with obtuse extremities, range (100) 8.0–12.4  $\times$  4.0–6.6  $\mu$ . Paraphyses outranking asci (Fig. 2: 5), filiform, septate, of equal diameter and unswollen or very slightly so at the tips.

Conidial stage not observed either in nature or in pure cultures.

Ascomatibus sparsis, solitariis vel gregariis, erumpentibus, initio subglobosis, dein cyathiformibus, cupulis humidulis planiusculis, margine in sicco semper connivente, breviter stipitatis, extus primitus distincte albidis, tomentosis, ciliatis, demum nudis, glabris; disco aurantiaco, vulgo 1–2 mm. diam.; pilis distincte elongatis, hyalinis, septatis, minute asperatis, 3  $\mu$  crassis. Ascis octosporis, clavatis, subcylindraceis, (150) 63.0–92.8  $\times$  6.0–12.0  $\mu$ , vulgo 70–80  $\times$  7–10  $\mu$ . Ascosporis monostichis, continuis, hyalinis, ovatis, (100) 8.0–12.4  $\times$  4.0–6.6  $\mu$ . Paraphysibus filiformibus, septatis, ascos superantibus, apice obtusis non sursum incrassatulis, guttulatis.

Fructificationibus conidicis non visis.

Hab. in ramulis emortuis *Pseudotsugae taxifoliae* in America Boreali. Specimen typicum 68062, *P. taxifolia*, in Mycological Collections, Bureau Plant Industry, U. S. D. A., Washington, D. C.

Habit. The type specimen, 68062, collected on dead branchlets or small branches of *Pseudotsuga taxifolia*, Portland Heights, Oregon, by J. R. Hansbrough, April 21, 1931, has been deposited in the Mycological Collections, Bureau Plant Industry.

Other specimens of the fungus on Douglas fir collected from 1930 to 1939 and deposited in the collections of the Division of Forest Pathology have been studied:

Oregon. 53094, Rhododendron, coll. G. G. Hahn; 68033, Rhododendron, coll. J. W. Kimmey; 68061, Rhododendron, coll. J. W. K. and T. W. Childs; K.100, Hood River, coll. J. E. Kienholz (Herb. J. E. K.).

British Columbia. 40502, Revelstoke, coll. J. R. Hansbrough; 40516, Owl Creek, coll. J. R. H.; 40531–32 Hunters Siding (Rosebery), coll. J. R. H.; 58002, Revelstoke, coll. J. L. Mielke.

This new species should not be mistaken for Dasyscypha Agassizii (Berk. & Curt.) Sacc. (8) with which it might be confused.

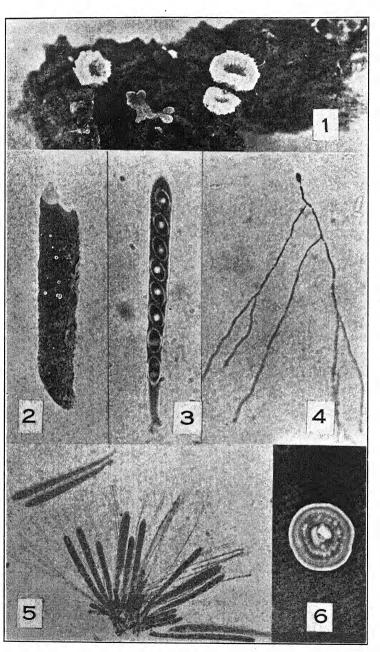


Fig. 2. Dasyscypha ciliata.

It differs from the latter species, which is found commonly in the eastern United States on balsam fir [Abies balsamea (L.) Mill.] and northern white pine (Pinus strobus L.), in spore characters and in the size of its fruit cups. An imperfect stage which is present in the life-history of D. Agassizii is apparently lacking in the life-history of this new Douglas fir species. In this, D. ciliata resembles the pine parasite, D. Pini, in whose life-history an imperfect stage has not been observed (4).

Dasyscypha ciliata is a saprophyte which is fairly uncommon, at least not present abundantly in the areas where it occurs. Unlike D. Agassizii, which grows not only on small branches, but also on large trunks, so far as we know D. ciliata is restricted in its growth to the small, shaded-out, dead branches and twigs of Douglas fir. In this respect, the saprophyte resembles the pine parasite, Atropellis pinicola Zeller & Goodding (Phytopathology 20: 555–567. 1930), and the European parasite of silver fir, Phomopsis abietina (Hart.) Wilson & Hahn (Brit. Myc. Soc. 13: 261–278. 1938), which likewise are confined to small parts. Investigation may show that certain of the factors influencing restricted colonization of both the saprophyte and the parasites, are identical.

#### CULTURE NOTES

Both of the new species described in this article grew slowly on 3 per cent synthetic malt agar, Dasyscypha ciliata being the slower. Ascospores of both species germinated readily on that medium within 24 hours and did not become uniseptate as did those of the large-spore Dasyscyphae (2, 4). It was found that D. Pseudotsugae could be maintained in culture without transfer for six months or more. D. ciliata on the other hand was found to stale in culture, and if it was not renewed by subculturing every third month, the colonies failed to grow when placed on a fresh maltagar substratum.

Dasyscypha Pseudotsugae. Germination of the ascospores was generally bipolar (Fig. 1:3) and took place within 24 hours. The initial characters of pure cultures of this species were very similar to those formed by D. ciliata on the same medium. On a German malt agar (7, p. 92) conidial stromata were formed within a week

in cultures made both from the inner diseased bark of the canker and from monoascus and -ascospore isolations. These conidial fructifications were also produced by the fungus growing in pure culture on sterilized Douglas fir twigs. The spores oozed from the pycnidia in opaque droplets or in light buff or pinkish buff spore-horns. Unlike those of the Dasyscyphae hitherto reported (2, 3, 4), the imperfect stage of D. Pseudotsugae is germinable. Germination also occurred within 24 hours and was both bipolar and monopolar (FIG. 1:5). Monoascus and -ascospore isolations of the species made September 13, 1930, which by 1938 had been subcultured 15 times, continued to produce germinable conidia. The writer found that these conidia, although somewhat desiccated after being kept in a culture tube for 10 months, germinated and produced culture characters identical with those obtained in fresh 1939 isolations of the perfect stage of the species. The fungus grew most readily and made a considerable whitish aerial growth on Douglas fir twigs. On synthetic malt agar, 2 month-oldmonoascospore colonies attained a diameter of 3.5 cm. colonies were distinctly zonate, roundish with even periphery; the aerial hyphae, fine, low growing, flocculent about the center, whitish becoming tinged with light-buff. In the substratum a warm buff color appeared and a tawny color formed below the inoculum (FIG. 1:6).

Dasyscypha ciliata. Germination was generally monopolar (Fig. 2: 4) although the bipolar type was occasionally observed. A roundish compact pompon-like colony consisting of fine, white, silky, aerial, low-growing hyphae formed slowly about the inoculum on the malt-agar slant. After one month roundish monoascospore colonies attained a diameter of 8 mm. These colonies had an even periphery and were indistinctly zonate. In two months the diameter enlarged to 18 mm. The whitish, aerial hyphae became tinged with light- to warm buff and in the substratum a burnt sienna or mahogany-red color was produced throughout (Fig. 2: 6). Conidial stromata were not observed in malt-agar cultures or on sterilized Douglas fir twigs.

#### SUMMARY

This paper presents the descriptions of two new species, Dasyscypha Pseudotsugae Hahn and D. ciliata Hahn on Douglas fir from the Pacific Coast.

Dasyscypha Pseudotsugae is a species definitely associated with cankers and roughened bark occurring on the living trunks and branches of saplings and trees of pole-size. The fungus occurs on Douglas fir, suppressed or growing on poor sites, in certain areas from California to British Columbia. The symptomatology of the Douglas fir canker is somewhat similar to that of the European larch canker.

Dasyscypha Pseudsotsugae has a conspicuous imperfect stage. The fungus is culturable from conidia which germinate readily within 24 hours. In this the species differs from the canker parasite, D. Willkommii on larch, for no one has succeeded in growing the latter from conidia.

Dasyscypha ciliata is a saprophyte occurring in the Pacific Northwest. Its growth is restricted to shaded-out, dead branches and twigs of small diameter. As far as known an imperfect stage is lacking in its life-history.

Culture notes dealing with the two new species are given.

For the photographs illustrating this article, I am indebted to Mr. C. K. Goodling, Division of Forest Pathology.

Division of Forest Pathology,

Bureau of Plant Industry,

in Coöperation with The Osborn Botanical Laboratory,

Yale University, New Haven, Connecticut

## EXPLANATION OF FIGURES

Fig. 1. Dasyscypha Pseudotsugae Hahn. 1, Typical canker on branch of suppressed Douglas fir sapling, collected at Lokoya, Napa County, California. Apothecia and imperfect stage are shown growing on diseased tissue. Approx. × 1.5; 2, Habit, on canker. Approx. × 10; 3, Mycelium produced in three days by a germinating ascospore on malt agar. Typical bipolar germination and the original ascospore at the center of the colony, are shown. Approx. × 344; 4, Conidial fructification with a droplet of exuding spores. Approx. × 10; 5, Five conidia on surface of malt agar, three days after germination. Both bipolar and monopolar germination types are shown. Approx. × 344; 6, Two-month-old monoascospore plate culture on malt agar. Nat. size.

Fig. 2. Dasyscypha ciliata Hahn. 1, Habit, on bark of dead branchlet of Pscudotsuga taxifolia. Approx. × 10; 2, Habit, both single and clustered apothecia. Nat. size; 3, Ascus with ascospores showing prominent guttules. Approx. × 800; 4, Mycelium produced in three days by germinating ascospore. Germination typically monopolar. Approx. × 344; 5, Asci and paaphyses. Approx. × 344; 6, Two-month-old monoascospore plate culture on malt agar. Nat. size.

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## THE OCCURRENCE OF FIVE SUCCESSIVE SWARMING STAGES IN A NON-SEXUAL ACHLYA <sup>1</sup>

S. B. SALVIN<sup>2</sup>

(WITH 1 FIGURE)

Diplanetism in the Saprolegniaceae was described for the first time in 1869 by Leitgeb (6), when he reported that in his genus Diplanes (now known as Saprolegnia) the zoöspores escaped from the sporangium as primary, pear-shaped, terminally biflagellate entities, swarmed for a period as such, encysted, either germinated by forming a hypha of germination or emitted a zoöspore of different structure—namely, reniform, laterally biflagellate—which in turn swarmed, encysted, and then gave rise to a germ tube.

The concept of the genus Achlya, originally established by Nees von Esenbeck (7) because of the presense of "Kügelchen . . . nach dem Austreten," has since been augmented on the basis that the zoöspores encysted immediately after emergence at the mouth of the sporangium in the form of a hollow sphere and later swarmed as laterally biflagellate cells, after which germination occurred. Such a mode of behavior has repeatedly been confirmed by a number of workers from 1872 on and is justly regarded as one of the main characteristics of the genus (2, 3, 8).

In the characterization of these and other genera of the Saprolegniaceae, the cycle of zoöspore swarming has been established as the basis of the generic concept. Under normal environmental conditions, the zoöspore cycles have been accepted as fairly constant, although under varying cultural influences minor changes have been reported to occur (1, 5). If the amount of nutrient present is above a certain threshold, the encysted spore germinates

<sup>&</sup>lt;sup>1</sup> Contribution from the Laboratories of Cryptogamic Botany and the Farlow Herbarium, Harvard University, no. 179.

<sup>&</sup>lt;sup>2</sup> The author expresses his indebtedness to Professor William H. Weston, Jr., under whose guidance and inspiration this work was carried on, for his most valuable suggestions and encouragement.

by a small tube which eventually forms a mycelium; but if the quantity of nutrient material is below this value, then the encysted zoöspore emits an active, laterally biflagellate swarmspore. There are other environmental factors, such as temperature and oxygen tension, which play an important role in determining whether the encysted spore gives rise to a hypha of germination or to an active, motile entity.

For many years, the cycles of zoöspores swarming in the various genera were considered alike in their end point—that is, they were terminated by a single swarming of secondary zoöspores. In 1919, however, Weston (9) reported in a non-sexual *Dictyuchus* that after the secondary, laterally biflagellate zoöspores had encysted, they might emit a second swarming stage. This repeated zoöspore emergence occurred under normal conditions, and as far as Weston was able to observe, the second set of laterally biflagellate zoöspores was exactly like the original one that had emerged from its unit within the sporangium. In 1932, also, Höhnk (4) reported a second emergence of laterally biflagellate zoöspores in *Saprolegnia torulosa* De Bary, and both a second and third in *Achlya racemosa* Hildebrand.

It therefore seemed of interest to determine the extent to which this repeated emergence of secondary or laterally biflagellate zo-ospores could be carried when environmental conditions were at an optimum for swarming. Accordingly, in this paper, there are presented observations showing that in a non-sexual, undetermined species of *Achlya* the usually described life cycle may be so modified as to include five successive swarmings before germination takes place. Since, to the writer's knowledge, such a degree of swarming has never before been reported, it appears desirable to record its occurrence in the following note.

The Achlya referred to in this paper was isolated from some mud gathered from a pond in the Blue Hills region of eastern Massachusetts. It was kept in culture for over eight months, and at no time displayed any evidence of sexuality, although zoösporangia were produced abundantly. Thus, it was impossible to determine the species exactly. Whether this condition was due to the fact that the species of Achlya was neutral or one of the strains of a heterothallic form has not been determined.

A pure culture was obtained from a single zoospore by picking up several encysted spores in a thin, sterile pipette, streaking them rapidly along the surface of a solid nutrient medium, and about

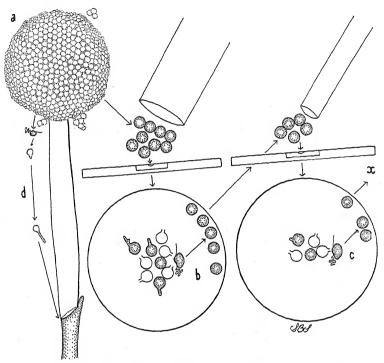


Fig. 1. Diagram illustrating quintuple emergence of the secondary zoospores in Achlya sp. The zoospores emerged from the sporangium to form a hollow sphere (a). The encysted spores were transferred by means of a pipette to a hanging drop, where the individual spores swarmed for a period and then encysted (b). These quiescent spores were then transferred with another pipette to a second hanging drop, where after a while they swarmed for a time, only to encyst again (c). Continuing from (x), the repeated emergence of secondary zoospores was carried on three additional times, making five swarming stages in all. At (d), the normal cycle is illustrated.

twenty-four hours later removing one of the resulting microcolonies onto another agar surface. A stock culture of the fungus was maintained on 0.3 per cent maltose-0.1 per cent peptone agar, but when zoöspores were desired, the fungus was transferred to a bit of hemp seed in glass-distilled water. The observations on the swarmings of the zoöspores were then made in a hanging drop in a depression slide. The mycelium in its morphological characteristics and the sporangium in its development were quite similar to those in other species of *Achlya*. The zoöspores, 16 micra long and 12 micra wide, were emitted in the usual manner, forming a somewhat irregular hollow sphere of encysted zoöspores, each 13 micra in diameter, at the sporangial apex. Each spore was uninucleate and contained several tiny refractive globules. If nutrient was lacking, each of these quiescent cells emitted a laterally biflagellate zoospore, which after a period of activity again encysted. This cycle of asexual spore formation agreed with the usual accounts. In the *Achlya* under discussion, however, when conditions were optimum, four additional emergencies of secondary zoöspores were seen to occur.

This sequence of events was revealed under the following conditions: A young sporangium with some of the attached hypha was cut from a mass of mycelium which was growing on a hemp seed in sterile water. This sporangium was then transferred to a hanging drop of well-aerated water kept at a temperature of about 15° C. In this drop, after the sporangium had matured in about  $2\frac{1}{2}$  hours, the zoöspores emerged from the terminal papilla to form a hollow sphere at the sporangium mouth (Fig. 1, a).

This spore ball was then transferred to the center of another similar hanging drop by means of a micropipette. The zoöspores began to emerge from the encysted state after about thirty minutes, swam about, and finally came to rest mainly along the edge of the suspended drop (Fig. 1, b). These encysted zoöspores from the edge of the drop were then transferred to another hanging drop of pure, cool, sterile, well-aerated water and their positions marked in order that there might be no possibility of confusing these with the ones that emerged and encysted subsequently. After about an hour and a half, while, to be sure, some of the zoospores germinated by sending out germ tubes, others emitted the characteristic secondary zoöspore. These in turn finally came to rest and encysted at the edge of the hanging drop (FIG. 1, c), whence, in the manner already described, they were transferred to the center of another similar drop. This process was repeated three more times, thus yielding a total of five successive swarmings of motile laterally biflagellate zoöspores. After the fifth emergence, the remaining

encysted zoöspores would apparently no longer emit a motile entity, for all germinated by sending out short hyphae of germination.

Five successive swarmings of the secondary zoöspore did not take place in every trial. In fact, out of six experiments, only two were characterised by this number of emergences, although every one did have some degree of repeated swarming. The zoöspores of the different swarming stages did not seem to vary in size or shape, although the amount of globular material in the zoospore seemed gradually to decrease.

The significance of this quintuple emergence of the laterally biflagellate zoöspore may be considered from various aspects. It obviously is of great survival value to the fungus. The active zoospore phase is able to continue over a much longer period of time and cover a far greater distance, thus increasing enormously its chances of finding a suitable substratum. Furthermore, this repeated swarming offers another example of "rejuvenation," in which a certain mass of protoplasm may enter into a quiescent state to emerge later as a thoroughly revived entity. If a zoöspore, on emerging from the encysted condition, is unable to find a suitable substance on which it may grow, it can pass again into a resting state, become rejuvenated, and then once more emerge as an active entity and have an opportunity of finding a favorable substratum on which it may form a germ tube and thus start a new colony. This quintuple swarming also adds to the evidence that the secondary, laterally biflagellate zoöspore is a far more efficient reproductive cell than the primary, terminally biflagellate one.

It is highly probable that the phenomenon of repeated emergence may be continued a still greater number of times if certain conditions are met. The water in which the experiments are carried on should be extremely pure, kept at a relatively low temperature (about 15° C.), and be well aerated. Since this rejuvenescence of motile zoöspores is dependent on stored energy and thus on reserve food material, other species may be found to have even more abundant storage material permitting a still greater number of emergence stages. It also appears that there may be some inherent factor present which in some way limits or controls the emergence of the zoöspores from the encysted state, since, under similar environmental conditions, the author, like Weston, was un-

able to induce the repeated emergence of zoöspores in *Thrausto-theca clavata* (De Bary) Humphrey.

In any case, the fact that in the present species of *Achyla* the writer succeeded in securing five swarming stages of secondary zoöspores, while hitherto the maximum number of emergences of motile laterally biflagellate entities was three, as reported by Höhnk in *Achlya racemosa* Hildebrand, seems to indicate that this aspect of asexual reproduction in the Saprolegniaceae is an interesting one worthy of further investigation.

#### SUMMARY

- 1. Observations on the zoöspore phase of an Achlya lacking sexual reproduction and therefore of an undetermined species were carried on under optimum conditions.
- 2. When the zoöspores are kept in cool, redistilled, well-aerated water, five successive swarmings of the secondary, laterally biflaggelate zoöspore have been observed to occur. Such a number of emergences is two more than has ever been reported in any species of the Saprolegniaceae.
- 3. The exact mechanism bringing about this repeated emergence is still in doubt, although it seems to involve both environmental and hereditary factors.

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## A NEW SPECIES OF TAPHRINA ON ALDER

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(WITH 2 FIGURES)

In a recent paper by the writer (4) several species of *Taphrina* occurring on various species of *Alnus* in North America were described and discussed. Received too late to be included in his paper was a new species of *Taphrina* causing leaf-curl of *Alnus rubra* Bong. The specimens, forwarded to the writer for study by Dr. Lee Bonar, were collected near Trinidad, Humboldt Co., California, March 24, 1931, by H. E. Parks.

According to the collector, the trees of Humboldt Co. are often seriously affected by the fungus. The infection is apparent on the leaves when they first appear in the spring, causing them to become greatly enlarged, often several times their natural size (FIG. 1). The leaves are curled and distorted and have a decided purple color. After the asci have matured and discharged their spores, the leaves shrivel, dry up and fall, and then a new crop of healthy leaves appears.

The discovery of a new species of Taphrina on Alnus rubra brings the total number of species on that host to three. The writer (4) has reported the bracts of the female catkins of this plant to be affected by Taphrina amentorum (Sad.) Rost. and T. occidentalis Ray. The two fungi affecting the female catkins, however, differ not only from one another, but also from the species occurring on the leaves. It has been noticed by the collector that Alnus rhombifolia Nutt. growing nearby does not become infected by the leaf-curling fungus.

The mycelium of the fungus affecting the leaves of A. rubra is confined strictly to the subcuticular region on the upper and lower surfaces. This mycelium constitutes the layer of ascogenous cells,

<sup>&</sup>lt;sup>1</sup> The writer wishes to express his appreciation to Dr. Lee Bonar for making the material available for study, and to Miss A. E. Jenkins for the loan of the specimen mentioned in the text.

each of which eventually develops into an ascus with the absence of a basal cell. The asci are cylindrical with rounded to truncate apices, and they measure 40–55  $\mu \times$  12–19  $\mu$  (FIG. 2B). The basal

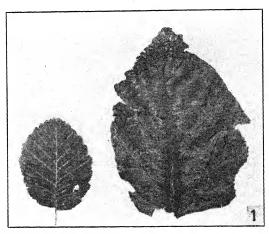


Fig. 1. Healthy leaf of Alnus rubra and leaf affected by Taphrina macrophylla, ½ nat. size.

portion of the ascus is often flat and occasionally may attain a width of  $32 \mu$ . Nearly all asci contain numerous spores, although a few were seen with eight.

Two leaf-invading species of Taphrina on Alnus japonica Sieb. and Zucc. have been reported from Japan. Both of these have asci lacking a basal cell, and in this respect they are like the species from California. The first of these, T. japonica, described by S. Kusano (1) has asci measuring 63–90  $\mu \times$  16–25  $\mu$ , whereas the second, T. Alni-japonicae, described T. Nishida (3) has asci 60–80  $\mu \times$  16–25  $\mu$ . Although the writer has not had an opportunity to compare these two species first hand, the host relationship and the similarity in size of the asci of the two species suggest that they may be identical. Mix (2) points out that these two Japanese species may be alike.

Specimens of *T. japonica* collected by S. Kusano near Tokyo, Japan, June 9, 1907 (communicated by Miss A. E. Jenkins), have been examined microscopically. The asci of this species are as described by Kusano (1) and are considerably larger than those

from the specimens collected in California (FIG. 2A). The basal portion of the asci is rounded and not widened as is often the case of the asci on the leaves of A. rubra. Kusano reports that T. japonica causes a "witches'-broom," whereas, the California species does not.

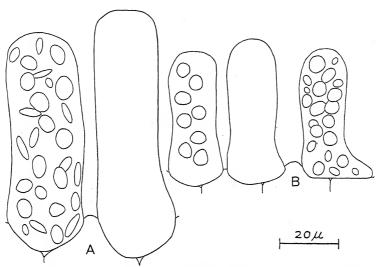


Fig. 2. A, asci and spores of  $Taphrina\ japonica;\ B$ , asci and spores of  $Taphrina\ macrophylla$ . Drawings made with the aid of a camera lucida;  $\times$  787.

On the basis of the morphology of the asci and the types of symptoms produced, the writer feels that the species affecting the leaves of *A. rubra* is distinct from *T. japonica* and has hitherto been undescribed.

Because of the large size of the leaf produced as a result of fungous invasion, the name suggested for the fungus is as follows:

## Taphrina macrophylla sp. nov.

Hymenio subcuticulari; mycelio interiore carente; ascis amphigenous, cylindraceis, in apice rotundatis aut truncatis,  $40-55~\mu$  longis  $\times$   $12-19~\mu$  crassis, circa  $48~\times$   $16~\mu$ ; ad basim rotundata vel complanata, usque  $32~\mu$  crassis; cellula basalari carente; sporidiis octonis vel multis, sphaeroideis vel ellipsoideis,  $2.5-5.5~\mu$   $\times$   $2-5~\mu$ .

Distribution: Causing leaf-curl and distortion of *Alnus rubra* in Humboldt Co., California, U. S. A.

Type: In the herbarium of the Department of Plant Pathology, Cornell University, No. 28831.

ISOTYPE: In the herbarium of the University of California, H. E. Parks No. 3592. Herbarium of W. W. Ray No. 500.

## SUMMARY

Taphrina macrophylla, a fungus causing a leaf disease of Alnus rubra in California, is described. The symptoms of the affected leaves likewise are described.

A comparison of this fungus with *Taphrina japonica* is made, and the differences and similarities of the two are indicated.

The host, Alnus rubra, is affected by three distinct species of Taphrina.

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## TWO NEW GASTEROMYCETES

JOHN B. ROUTIEN

(WITH 23 FIGURES)

## GASTERELLOPSIS SILVICOLA

During the summer of 1938 the author collected a number of soil samples near near East Lansing, Michigan, to determine whether or not *Gasterella lutophila* Zeller & Walker could be found. The results of that study may be found in a previous paper.¹ In addition to *G. lutophila*, fruiting-bodies of another fungus developed during the last of July, 1938, on one of the soil samples that came from a particular wood-lot. On October 11 samples of soil were obtained in triplicate from the same spot from which the earlier sample had been taken. Fruiting-bodies of this same new fungus were first observed on one of these collections on October 29. On a second lot of the soil fruiting-bodies did not appear until November 7, 1938.

The methods of study were the same as those employed for Gasterella lutophila.

Because of its similarity in many particulars to Gasterella the writer suggests the generic name Gasterellopsis for this new fungus.

The basidiocarps of Gasterellopsis were first visible on the surface of the soil in from 18 to 26 days after the soil was collected and prepared. The first sign of the fungus was the appearance of minute wefts of loose, white hyphae. These developed into the mature fruiting-bodies in four to six days. Most of the specimens developed on the surface of the soil, but occasionally a specimen formed just below the surface and pushed the soil particles aside as it grew.

A scarcity of specimens between the youngest and mature stages prevented discovery of the details of development of the glebal

<sup>&</sup>lt;sup>1</sup> Routien, John B. Observations on Gasterella lutophila. Mycologia 31: 416-418. 1939.

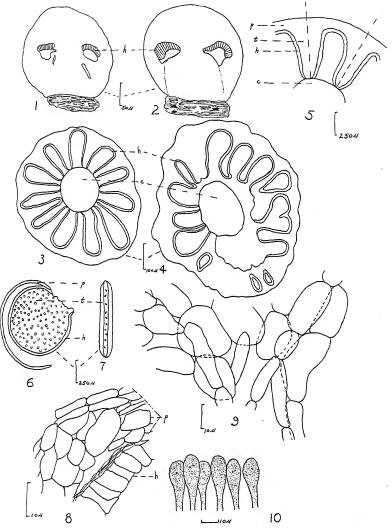
chamber. However, it seems that the cavity develops in the manner outlined below.<sup>2</sup>

The youngest sectioned specimens were  $200\,\mu$  in diameter. In them the hymenium was just beginning as a layer of darkly-staining, downward-directed cells (Fig. 1, h). The cells of this layer were two-nucleate. Below this young hymenial layer there was a small circular cavity around a columella. In some young specimens (Fig. 2) it appeared as if the glebal cavity may form as a result of the tearing of tissue below the young hymenium as the fruiting-body increases in size. As the basidiocarp grows this cavity becomes enlarged.

At the same time that the basidiocarp is enlarging, tramal plates begin to develop. Apparently they originate as outgrowths of hymenium-bearing tissue from the walls of the glebal cavity. It could not be definitely established, but it seems that any particular infolding develops downward from the top, inward from the side and upward from the bottom of the basidiocarp. In the fruiting-bodies secured in the late fall all of the infoldings eventually had grown centripetally into contact with the columella, thus dividing the originally simple cavity into several distinct radially-arranged cavities (Fig. 3). In those specimens secured in the summer there were many mature fruiting-bodies in which some of the tramal plates extended from a third to a half of the distance toward the columella (Fig. 4). In some of these basidiocarps small hymenial cavities interspersed between tramal plates were also found (Fig. 4).

A peculiar feature of the fungus was discovered during observation of the living fruiting-bodies. It was found that the basidiocarp (with the exception of the columella) could easily be broken into 12–14 segments. Each segment was formed by the splitting of adjoining tramal plates (as indicated by the broken line in figure 5). Thus the sides of the peridiole-like segments were the torn or exposed tramal tissues (Fig. 6). The appearance in any segment of the edge next to the columella can best be explained by reference to the drawing of such a structure (Fig. 7).

<sup>&</sup>lt;sup>2</sup> In a personal communication Dr. Leva B. Walker has informed the writer of the manner in which the basidiocarp of Gasterella lutophila develops. The stages of the development of Gasterellopsis can be interpreted in the same manner.



Figs. 1-10. Gasterellopsis silvicola.

Most of the mature fruiting-bodies measured 2 mm. in diameter, but a few were smaller. None, however, were smaller than 1 mm. With the maturation of the fruiting-bodies the spores became dark. As a result the basidiocarps appeared grayish when mature. Soon after the spores darkened, groups of filaments of the peridium began to project from the surface of the basidiocarp as a result of

failure to grow while the basidiocarp was increasing in size. At this stage the peridium could very easily be removed from all of the fruiting-body except the top.

The mature fruiting-body consists of a peridium, a single glebal cavity traversed lengthwise through the center by a columella that is continuous with the fruiting-body at the top and tramal plates that project from the wall of the cavity to or almost to the columella. The hymenium covers all surfaces of the cavity except the columella.

The peridium is  $18-25 \mu$  thick and is composed of more or less inflated cells (Figs. 8, 9) in the form of distinct hyphae.

The columella is evident in the youngest basidiocarp sectioned (FIG. 2). In a mature fruiting-body it is much taller and thicker (FIGS. 3, 4, 11, 12, 13). Although it seems to be continuous with the top of the basidiocarp, the columella is very easily pulled out from the fruiting-body because of the weakness of the flesh. This often happens when the specimens are being removed from the soil. The columella is composed of longitudinally-directed hyphae.

The tissue at the base of the fruiting-body is apparently quite weak. This is indicated by the fact that the columella is so easily removed and by the fact that the adjoining tissue becomes loosened from the base of the columella (FIGS. 11, 12, 13). The edges are then pulled away from the columella in such a manner that the basidiocarp looks very much like a diminutive mushroom.

When the fruiting-bodies were as much as six days old the cells of the peridium dissolved. This left the subhymenial layer exposed. At the same time dissolving of the tramal plates into a moist mass left the glebal cavity empty except for the spores. As a consequence of these changes, the mature basidiocarp becomes unilocular.

The hymenium consisted of paraphyses and basidia. In the youngest specimen studied most of the cells of the developing hymenium possessed two nuclei each. In the same specimen uninucleate basidia were found (Fig. 10). Nuclei in the basidia were not seen in the process of division. However, two-nucleate and four-nucleate basidia were observed (Fig. 14); the nuclei in the latter case were  $1.3\,\mu$  wide. In a few basidia six nuclei were observed.

The basidia bore 2–4 basidiospores. It seemed that whenever two spores were formed, two nuclei remained in the basidium (FIG. 15). In at least some cases, when there were four spores to each basidium, four nuclei remained in the basidium (FIG. 17). All of this, of course, indicates that the four nuclei formed by the meiotic divisions may divide once more.

The basidiospores are citriform, apiculate, brownish-black and verrucose (FIG. 18). Each spore is provided with a pedical that measures  $2.0 \times 1.5 \,\mu$ . Spores of the fruiting-bodies collected in the fall measured 14.5 (16.5)–18  $\times$  11 (13)–14.5  $\mu$ , but the spores of the fruiting-bodies collected in the summer measured 13.5 (14.6)–16.2  $\times$  10.8 (11.2)–12.6  $\mu$ . All of these measurements were made from permanent slides of the fungus.

It might be suggested that this fungus is a depauperate *Coprinus*. It does resemble that genus in several respects. The structure of the cells of the peridium, the origin of the circular glebal cavity around the columella and the dissolving of the trama are similar in the two genera. However, *Gasterellopsis* is unlike *Coprinus* in that in the former genus the dissolved trama does not form a liquid, the basidia are not like those of *Coprinus*, there is a splitting centripetally through the tramal plates rather than between them as is possible in *Coprinus* and the spores are not at all like those of *Coprinus*.

The fungus here described is much like Gasterella. The basidiocarp appears to develop in a similar manner in regard to the origin of the hymenium, and the spores are of the same type. The fungi differ, however, in several other points. The peridium of Gasterella is of filamentous cells, but in Gasterellopsis it is made up of inflated cells. The greatest differences are the presence, in Gasterellopsis, of tramal plates, an annular cavity and a columella as well as the opening of the basidiocarp at the base and the dissolving of the peridium and tramal plates.

In spite of these differences Gasterella and Gasterellopsis appear to the writer to be sufficiently alike to warrant their inclusion in the same family. When Gasterella was described,<sup>3</sup> it was stated that it "... should doubtless be referred to a new family, but

<sup>&</sup>lt;sup>3</sup> Zeller, S. M. & Leva B. Walker. *Gasterella*, a new uniloculate Gasteromycete. Mycologia 27: 572-579. 1935.

we prefer now to include it in the Protogastraceae." Since Gasterella seems to be sufficiently different from Protogaster to warrant its being placed in a new family apart from the Protogastraceae, and since there is now another plant which agrees even less with the description of the Protogastraceae 4 than does Gasterella, the writer makes the suggestion that Gasterella and Gasterellopsis should be placed in a new family, the Gasterellaceae.

The final disposition of such a family must wait until careful study of all possibly related forms has been made, but at present it seems that the Gasterellaceae would be placed near the Hymenogastraceae and Hydnangiaceae.

In agreement with the growing tendency of some of the recent students of the Ascomycetes as well as of the Basidiomycetes, the author believes that much greater importance should be assigned to similarities and differences in spore structure in the Gasteromycetes. It is quite possible that there have arisen parallel series of morphological development, each series being characterized by a distinct type of spore. Perhaps this will be suggested in some revised classification of the Gasteromyceteae. In that case the Protogastraceae and the Gasterellaceae (if the family is established) would be the primitive (or terminal?) families of parallel series of development in different orders in which the spore type would be of major importance.

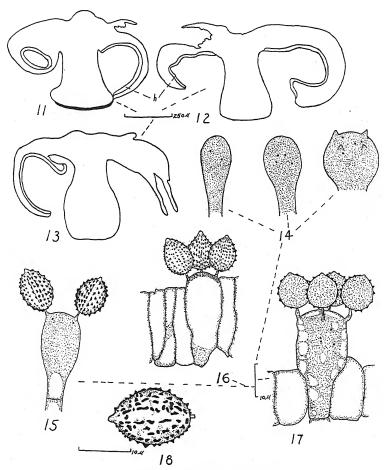
## Gasterellopsis gen. nov.

Fructificationes minutae, subsphaericae; peridium ex cellulis inflatis compositum, dehiscens circumscissim ad basim; gleba uniloculata cum invaginationibus centripetalibus verticalibus paene sine usque columellam attingentibus; columella percurrens totam fructificationem ad apicem; sporae citriformes, apiculatae, verrucosae, brunnae-nigrae.

Fructifications small, subspherical; peridium of inflated cells, dehiscent in a circumscissle manner at the base; gleba uniloculate with vertical centripetal infoldings that reach usually to the columella; columella central, percurrent; spores citriform, apiculate, verrucose, brownish-black.

The type species is Gasterellopsis silvicola.

<sup>4</sup> Zeller, S. M. *Protogaster*, representing a new order of the Gasteromycetes. Ann. Missouri Bot. Gard. 21: 231-249. *illust*. 1934.



Figs. 11-18. Gasterellopsis silvicola.

## Gasterellopsis silvicola sp. nov.

Fructificationes oblate sphaericae, 1–2 mm. diametro, primum albae demum nigrescentes; peridium dehiscens de basi columellae, ad maturitatem deliquescents; laminae demum deliquescentes; basidia clavata, 2- vel 4-spora; sporae  $14.5(16.5)-18 \times 11(13)-14.5~\mu$ ; pedicello  $2 \times 1.5~\mu$ .

Ad terram uvidam ex silva, East Lansing, Michigan.

Fructifications spherical to depressed, 1–2 mm. in diameter, white, then black; peridium dehiscent at the base of the columella, dissolving at maturity; tramal plates finally dissolving; basidia clavate, 2–4 spored; spores 14.5 (16.5)–18  $\times$  11 (13)–14.5  $\mu$ ; pedicels measuring 2  $\times$  1.5  $\mu$ .

On soil that was brought into the laboratory from the woods near East Lansing, Michigan. November, 1938. Type in herbarium of the author. Isotypes with Dr. S. M. Zeller.

Since cultures of Gasterellopsis would be desirable, attempts were made to germinate the spores of this fungus. The spores were plated out in potato-dextrose agar, soil-decoction malt agar, acidified potato-malt agar and acidified potato-dextrose agar. Spores also were placed in potato-dextrose broth and in solutions of 3-indoleacetic acid. This last solution was used in two concentrations: (1) 50 mg. per liter and (2) 25 mg. per liter of solution. Attempts were made to secure tissue cultures by placing bits of tissue with some of the spores in each of the media mentioned above.

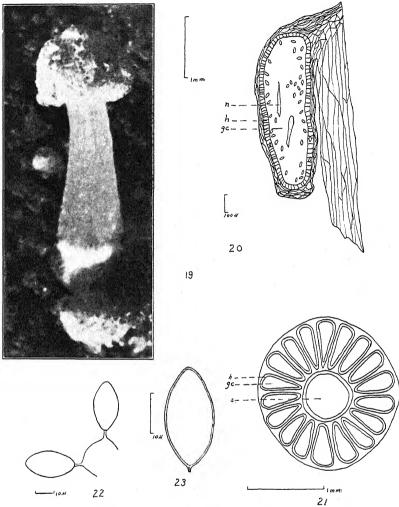
No growth of the hyphae or germination of the spores was obtained.

## SECOTIUM COPRINCIDES

In the discussion of Gasterellopsis silvicola it was mentioned that the fungus developed only on two of the soil samples that were secured in triplicate on October 11, 1938. On the third sample there began to develop on November 12, 1938, two fruiting-bodies that greatly resembled Gasterellopsis. However, the fruiting-bodies became larger than that fungus and on November 15 one of them developed a stalk that elevated the fungus into the air. The other fruiting-body formed a short stalk that did not elongate. These were the only specimens that developed on this lot of soil.

The other two samples (on which only Gasterellopsis had formed) were again saturated with water on December 12 and the cover placed over the container. By January 12, 1939, fruiting-bodies of Gasterellopsis had developed on both samples. On one of the samples more specimens of the new fungus, to which the name Secotium coprinoides was later applied, developed: one on January 26 and one on February 3.

Some of the material was killed in formol-acetic-alcohol and prepared for sectioning and staining. Since this fungus in its earliest stages of growth looked like *Gasterellopsis*, it was impossible to secure young specimens for study of the development of the fruiting-body. All of the information regarding the fungus, therefore, is limited to the mature plant.



Figs. 19-23. Secotium coprinoides.

## Secotium coprinoides sp. nov.

Fructificationes albae, 4 mm. alto; peridium album, 25–35  $\mu$  crassitudine, ex cellulis filamentosis inflatis; loculi glebales circa 18; basidia 2- vel 4-spora paraphysibus intermixta; sporae ellipsoideae, leves, nigrae,  $18(23.5)-30.5 \times 12.6(12.75)-16\,\mu$ ; pedicello  $2\times 1.5\,\mu$ .

Ad terram uvidam ex silva. East Lansing, Michigan.

Fructifications (FIG. 19) 4 mm. tall, white, consisting of a stalk and a pileus-like upper portion nearly 2 mm. in diameter; this up-

per fertile region united to the stalk only near the apex of the latter (Fig. 20) and consisting of about 18 glebal chambers (Figs. 20, 21); peridium white, of filamentous-inflated cells, 25–35  $\mu$  in thickness; hymenium at maturity consisting of basidia and paraphyses; basidia 2–4 spored (Fig. 22); spores (Fig. 23) elliptical, smooth, black, measuring (in fresh, unkilled specimens) 18 (23.5)–30.5  $\times$  12.6 (12.75)–16  $\mu$ , each spore with a pedicel measuring 2  $\times$  1.5  $\mu$ ; two, three or four spores not uncommonly grown together and united in a group.

Developing on soil brought into the laboratory from the woods near East Lansing, Michigan, November, 1938. Type specimens in herbarium of the author.

This fungus resembles both *Gasterellopsis* and *Coprinus*. From the former it is distinguished by the stipe, the presence of a number of glebal chambers and the type of spore. From the latter it is distinguished by the presence of glebal chambers, the acrogenous position of the spores and the presence of a pedicel on each spore.

There seems to be no *Secotium* to which this new species might be closely related. *S. melanosporum* Berk. has black spores, but the fruiting-body is quite large. *S. olbium* Tul. is described as being 4–6 mm. high, but the spores are smaller than those of *S. coprinoides* and are spherical and rugulose.

#### ACKNOWLEDGMENTS

The writer wishes to acknowledge the kind assistance and advice of Dr. E. A. Bessey during the progress of this study and in the interpretation of data and preparation of this paper. He also is grateful to Dr. S. M. Zeller and Dr. Leva B. Walker for their helpful suggestions. Appreciation is expressed to Professor F. C. Strong for taking the photograph of the fruiting-body of Secotium coprinoides.

DEPARTMENT OF BOTANY,
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#### EXPLANATION OF FIGURES

Figs. 1-18 are of Gasterellopsis silvicola. (c) is the columella, (h) the hymenium, (p) the peridium and (t) the trama. Fig. 1, median, longitudinal section through a young fruiting-body; 2, a similar section through

an older specimen; 3, median, transverse section through a mature fruiting-body; 4, similar section showing some of the shorter tramal plates and the small, imbedded glebal chambers; 5, diagram of part of a fruiting-body indicating by the broken line how the tramal plates may be split; 6, one of the segments formed by the centripetal splitting of adjoining tramal plates; this also shows how the peridium may be removed; 7, a segment as it appears from the side next to the columella; 8, a portion of the peridium and hymenium of a mature fruiting-body in which the spores have been released from the basidia; 9, cells of the peridium; 10, basidia from a young fruiting-body showing the fusion nuclei and the nuclei formed in the first meiotic division; 11–13, mature fruiting-body; 14, two- and four-nucleate stages of meiosis; 15, two-spored basidium with two nuclei remaining in the body of the basidium; 16, three-spored basidium; 17, four-spored basidium with four nuclei in the body of the basidiospore.

Figs. 19-23 are of Secotium coprinoides. Fig. 19, mature fruiting-body; 20, a portion of the mature fruiting-body in a median, longitudinal section through a glebal cavity; (n) is part of a nematode; 21, median, transverse section through a mature fruiting-body showing the stipe (s) and the glebal chambers (gc); 22, two-spored basidium showing acrogenous position of

the spores; 23, basidiospore.

## A NEW CERCOSPORA ON LIPPIA CARDIOSTEGIA <sup>1</sup>

B. H. Davis 2

(WITH 1 FIGURE)

The species of *Cercospora* described herein was found among unidentified fungous collections made by Dr. W. A. Kellerman in Guatemala in 1906 on *Lippia cardiostegia* Benth. An examination shows this to be specifically distinct from Cercosporae described on this or closely related genera. The Guatemalan *Cercospora* differs from *C. Lippiae* described by Ellis and Everhart <sup>3</sup> on *Lippia nodiflora* (L.) Michx. in the indefinite spots produced in its hypophyllous fruiting, dark colored conidiophores, and wide, colored conidia (FIG. 1). The following name is proposed:

## Cercospora Cardiostegiae sp. nov.

Maculae indefinitae, superficie supera dilute brunneo; fungus hypophyllum, effusum, parva atra loca formans; stromata absunt vel parva, atro-fuscis; conidiophoris non-fasiculatis vel 2-12 in fasciculo, dilute ad mediocriter olivaceum brunneum, frequenter flexuosis, 1-5 septatis, interdum leniter ad septa constrictis, non-fasciculatis conidiophoris frequenter ramosis, erectis ad curvatas, 1-4 leniter ad abruptum geniculatum, apicibus rotundatis, sporarum cicatricibus parvis, 4-6.5  $\times$  15-60  $\mu$ , plerumque 5.5-6  $\times$  40-50  $\mu$ ; conidiis dilute ad mediocriter olivaceum brunneum, rectis vel curvulis, cylindraceis ad cylindrum obclavatum, 1-7 conspicuiter septatis, plerumque 1-3 septatis, interdum ad septa constrictis, extremis abrupte rotundatis ad obconica, 4-5.6  $\times$  20-75  $\mu$ , plerumque 4.2  $\times$  25-40  $\mu$ .

Hab. in foliis Lippia cardiostegia Benth., Laguna, Depart. Amatitlan, Guatemala.

No definite leaf spots formed, upper surface light-brown; fruit-

- <sup>1</sup> Papers from the Department of Botany, The Ohio State University, No. 422.
- <sup>2</sup> The writer wishes to express his appreciation of the generous help of Dr. Charles Chupp in describing the species and in making available type specimens for examination. Thanks are due Dr. H. N. Moldenke of the New York Botanical Garden for his kindness in identifying the host plant.

<sup>3</sup> Ellis, J. B. & Everhart, B. M. Cercospora Lippiae E. & E. In Additions to Cercospora, Gloeosporium and Cylindrosporium. Jour. Myc. 3: 20. 1887.

ing hypophyllous, effuse, forming small darkened areas; stromata absent or small, dark-brown; conidiophores non-fasciculate or 2–12 in a fascicle, pale to medium olivaceous-brown, frequently irregular

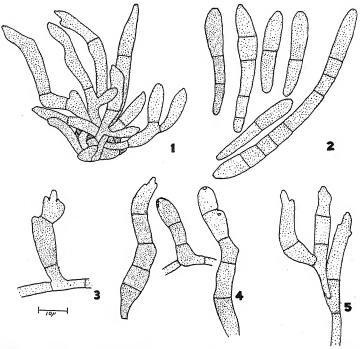


Fig. 1. Cercospora Cardiostegiae. 1, stroma and conidiophores; 2, conidia; 3, 4, simple conidiophores; 5, branched conidiophore.

in width, 1–5 septate, sometimes slightly constricted at the septa, non-fasciculate conidiophores frequently branched, straight to variously curved, 1–4 mildly to abruptly geniculate, tips bluntly rounded, spore scars small,  $4-6.5 \times 15-60 \mu$ , usually  $5.5-6 \times 40-50 \mu$ ; conidia pale to medium olivaceous-brown, straight to slightly curved, cylindrical to cylindro-obclavate, 1–7 plainly septate, usually 1–3 septate, sometimes constricted at the septa, ends bluntly rounded to obconical,  $4-5.6 \times 20-75 \mu$ , usually  $4.2 \times 25-40 \mu$ .

On leaves of *Lippia cardiostegia* Benth., Laguna, Depart. Amatitlan, Guatemala.

Type material deposited in herbaria of Ohio State University and Cornell University.

DEPARTMENT OF BOTANY,
OHIO STATE UNIVERSITY

# ASCOMYCETES FROM THE STATE OF MINAS GERAES (BRAZIL)

CARLOS E. CHARDON, JULIAN H. MILLER AND ALBERT S. MULLER (WITH 37 FIGURES)

The present paper on the Ascomycetes from the State of Minas Geraes, Brazil, is based almost exclusively on collections made by the junior author, who held the chair of phytopathology at the Escola Superior de Agricultura, at Vicosa, during the years 1929 to 1937.

These collections comprise about 1150 numbers, which have been kept at the herbarium of the school at Vicosa, and duplicates deposited in the herbarium of the Department of Plant Pathology at Cornell University.

The rusts of the collection have been recently studied by Dr. Frank D. Kern and Dr. W. H. Thurston of the Pennsylvania State College. The Cercosporae, constituting an important group of plant parasites, were abundantly collected and two contributions have appeared by Dr. Charles Chupp, of Cornell University and the junior author. These two papers enumerate 123 species of Cercospora, 22 of which are new to science.

The present paper lists 114 species, 21 of which are described as new. The species of *Balansia*, *Claviceps*, *Dothichloe* and *Myriogenospora* have been determined by Dr. Wm. W. Diehl, of the United States Department of Agriculture; and the Perisporiales and Microthyriales, by Professor R. A. Toro, of the University of Puerto Rico. The writers wish to express their acknowledgments to the above collaborators.

#### MYRIANGIALES

1. Myriangium Duriaei Mont. & Berk. Lond. Jour. Bot. 4: 72. 1845.

On scale insect on Prunus Persica, Vicosa, Muller 141, Mar. 3, 1930.

<sup>1</sup> Archives Inst. Biol. Rio 1<sup>3</sup>: 213-220. 1934; 3<sup>1</sup>: 91-98. 1937.

#### PERISPORIALES

2. Capnodium Citri Berk. & Desm. Jour. Hort. Soc. Eng. 4: 252. 1849.

On Citrus sp., Vicosa, Muller 188, Feb. 3, 1930.

3. Capnodium Theae Boedijn Bull. Jard. Bot. Buitg. III 11: 223. 1931.

On Thea sinensis, Ouro Preto, Muller 527, May 1, 1933.

- 4. Meliola Mataybae F. L. Stevens, Ann. Myc. **26**: 226. 1928. On *Paullinia* sp., Vicosa, *Muller* 553, May 25, 1933.
- 5. Meliola Mulleri Toro, sp. nov.

Type: Cornell Univ. Explor. Brazil 632.

Mycelii plagulae epiphyllae, orbiculares, .5–1.5  $\mu$  in diam., hyphis centrifugis, ramosis, fuscis, septatis, parietibus crassis, setis mycelicis acutis,  $266 \times 7 \,\mu$ , dilutis brunneis, septatis, rectis; hyphopodiis capitatis alternantibus, clavatis, cellula superiore globosa,  $10 \,\mu$  in diam., cellula inferiore rectangulare; hyphopodiis mucronatis ampulliformibus, continuis, oppositis,  $13 \,\mu$  altis; perithecia globosa, in plagulis centraliter disposita, pauca lenia, leniter translucida,  $120 \,\mu$  in diam.; asci fugacea, sporis oblongis, utrinque obtusis, 4-septatis,  $95 \times 30 \,\mu$ .

Mycelial colonies epiphyllous, round, .5–1.5 mm. in diam., with hyphae growing centrifugally, branched, brown, septate and thickwalled; mycelial setae acute,  $266 \times 7~\mu$ , light brown throughout, septate, straight; capitate hyphopodia alternate, pear-shaped, upper cell round,  $10~\mu$  in diam., lower cell rectangular,  $7~\mu$  wide, forming an acute angle with the mycelium; mucronate hyphopodia bottle shaped, one-celled, opposite,  $13~\mu$  high; perithecia in center of spot, few, smooth, slightly translucent,  $120~\mu$  in diam., with evanescent asci; spores 4-septate, oblong, end cells rounded,  $95 \times 30~\mu$ .

Beelian formula : - 3111-63:21.

On Cardiospermum grandiflorum, Ana Florencia, Muller 632, June 21, 1933.

- 6. Meliola Panici Earle, Muhlenbergia 1: 12. 1901. On *Erianthus angustifolium*, Vicosa, *Muller 579*, June 3, 1933.
- 7. Meliola Teramni Sydow H. & P. Ann. Myc. 15: 193. 1917. On *Teramnus uncinatus*, Vicosa, *Muller 269*, May 2, 1931.
- 8. Meliola Thouiniae Earle, Bull. N. Y. Bot. Gard. 3: 308. 1905.

On Serjania sp., Vicosa, Muller 552, May 25, 1933.

9. Parodiopsis Brachystegiae (P. Henn.) Arn. Annal. des Epiphyties 7: 68–70, 1924.

On Copaiba Longedorffii, Vicosa, Muller 723, Feb. 15, 1934.

#### HYPOCREALES

10. Balansia Ambiens Moll. Phycom. und Ascomycet. 303. 1901.

On Leersia grandiflora, Vicosa, Muller 415, Mar. 22, 1933.

11. Claviceps Paspali Stev. & Hall, Bot. Gaz. **50**: 462. 1910. On *Paspalum intermedium*, Uberaba, *Muller 1091*, May 19, 1936.

On Paspalum mandiocanum, Vicosa, Muller 434, Mar. 30, 1933.

On Paspalum pilosum, Curvello, Muller 1012, Mar. 1, 1936.

On Paspalum plicatulum, Curvello, Muller 1013, Mar. 1, 1936.

On Paspalum plicatulum var. cinereum, Uberlandia, Muller 1015, Mar. 14, 1930.

12. Dothichloe atramentosa (Berk. & Curt.) Atk. Jour. Myc. 11: 260. 1905.

On Andropogon bicornis, Vicosa, Muller 19, Nov. 10, 1929.

On Andropogon leptostachyus, Vicosa, Muller 473, Apr. 18, 1933.

On Sporobolus Poirctii, San Geraldo, Muller 1137, Nov. 17, 1929.

13. Dothichloe discoidea (P. Henn.) Diehl, comb. nov. Balansia discoidea P. Henn. Hedwigia Beibl. 39: 77. 1900.
On Ichnanthus candidus, Vicosa, Muller 475, Apr. 18, 1933.
On Oplismenus hirtellus, Vicosa, Muller 641, Apr. 18, 1933.

On Panicum sp., Metallurgica, Muller 1136, Dec. 23, 1929.

On Function sp., Metanurgica, Mutter 1750, Dec. 25, 1929.

14. Dothichloe Limitata Diehl, Jour. Agr. Res. 58: 948. 1939.

On Sporobolus indicus, Ana Florencia, Muller 768, Apr. 1, 1934, and Sylvestre, Muller 37, Dec. 1, 1929.

15. Dothichloe Nigricans (Speg.) Chardon, Mycologia 19: 296. 1927.

Epichloc nigricans Speg. Anal. Soc. Ci. Argent. 19: 47. 1885.

On Panicum affolyroides, Uberlandia, Muller 1064, May 18, 1936.

On Panicum Schiffneri, Vicosa, Muller 490, Apr. 22, 1933.

- 16. Dothichloe subnodosa Chardon, Mycologia 13: 287. 1921. On *Panicum pilosum* Vicosa, *Muller 411*, Mar. 22, 1933.
- 17. Gibberella Pulicaris (Fries) Sacc. Michelia 1: 43. 1879 Sphaeria pulicaris Fries, Syst. Myc. 2: 417. 1823.

On Coffea arabica, Vicosa, Muller 706, Jan. 3, 1934.

On dead sticks, Ponta Nova, Muller 261, Apr. 4, 1931.

18. GIBBERELLA SAUBINETII (Mont.) Sacc. Michelia 1: 513. 1879.

Sphaeria Saubinetii Mont. Crypt. Alger. 1: 476. 1846.

On Oryza sativa, Vicosa, Muller 946, June 22, 1935.

On Paspalum intermedium, Vicosa, Muller 945, June 22, 1935.

On Triticum aestizum, Vicosa, Muller 148, Feb. 20, 1930.

On Zea Mays, Vicosa, Muller 311, Feb. 25, 1932.

19. LINEARISTROMA LINEARE (Rehm.) Höhnel Sitz.-ber. Akad. Wien 119: 939. 1910.

On Axonopus sp., Sao Miquel, Vicosa, Muller 1135, Nov. 15, 1929.

20. Myriogenospora aciculispora Viz. Bol. Agr. Sao Paulo 27: 60-69. 1926.

On Saccharum officinarum, Vicosa, C. A. Drummond 1270, June 8, 1938.

21. Myriogenospora Paspali Atk. Bull. Torrey Club 21: 225. 1894.

On Axonopus obtusifolius, Vicosa, Muller 77, Dec. 20, 1929.

On Imperata brasiliensis, Vicosa, Muller 28, Nov. 20, 1929.

On Papsalum conjugatum, Vicosa, Muller 488, Apr. 22, 1933.

22. NECTRIA CINNABARINA Tode ex Fries, Summa Veg. Scand. 388. 1849.

On Morus alba, Vicosa, Muller 1032, Jan. 15, 1936.

23. Nectria conigena Ellis & Ev. Bull. Torrey Club 10: 77. 1883.

On Crotalaria juncea, Vicosa, Muller 454, Apr. 12, 1933, and Muller 973, June 15, 1935.

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- 24. Nectria sanguinea Fries, Summa Veg. Scand. 388. 1849.
  On Citrus sp., Muller 1140, Lavras, Dec. 4, 1936.
  On bark, Ponte Nova, Muller 258, Apr. 4, 1931.
- 25. Pleonectria pseudotrichia (Schw.) Wollen. Angew. Bot. 8: 195, 208. 1926.

Sphaeria pseudotrichia Schw. Berk. & Curt. Jour. Acad. Phila. II. 2: 289. 1853.

Megalonectria pseudotrichia Speg. Anal. Soc. Ci. Argent. 12: 217. 1881.

On dead wood, Vicosa, Muller 887, Mar. 20, 1935.

26. Podonectria coccicola (Ellis & Ev.) Petch, Trans. Brit. Myc. Soc. 7: 146. 1921.

On Citrus sp., Vicosa, Muller 47, Oct. 6, 1929, and Muller 53, Oct. 13, 1929.

27. Sphaerostilbe flammea (Berk. & Rav.) Tul. Fung. Carp. 1: 130. 1861.

On Ficus Carica, Vicosa, Muller 136, Oct. 12, 1929.

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- 28. Apiospora Apiospora (Dur. & Mont.) Underw. & Earle, Bull. Ala. Exp. Sta. 80: 186. 1897.
  On bamboo cane, Vicosa, Muller 397, Jan. 28, 1933.
- 29. CERATOSTOMELLA FIMBRIATA (Ellis & Hals.) Elliott, Phytopathology 13: 56. 1923.
  On Crotalaria juncea, Vicosa, Muller 1096, Apr. 12, 1936.
- 30. Diatrype Riograndensis Rehm, Ann. Myc. 9: 368. 1911. On wood, Ponte Nova, Muller 256, Apr. 4, 1931. On wood, Vicosa, Muller 496 and 500, Apr. 23, 1933.
- 31. DIAPORTHE CITRI Wolf, Jour. Agr. Res. 33: 625. 1926. On Citrus aurantifolia, Vicosa, Muller 842, Jul. 28, 1934.
- 32. Eutypella fraxinicola (Cooke & Peck) Sacc. Syll. Fung. 1: 154. 1882.

On dead branches, Vicosa, Muller 495, Apr. 23, 1933. On dead wood, Drummond 1117, Feb. 15, 1936. This is a very common species with spores  $6-9 \times 2 \mu$ , and slightly protruding coarsely sulcate ostiola. It occurs on almost any kind of deciduous wood and so has been listed under many names. The correct specific name awaits a revision of the genus.

33. Eutypella stellulata (Fries) Sacc. Syll. Fung. 1: 149. 1882.

On Montanua grandiflora, Vicosa, Muller 766, Mar. 27, 1934. This species differs from the above only in the possession of larger ascospores. It also is very common in most countries.

34. Fracchiaea Heterogena Sacc. Atti Soc. Ven.-Trent. 2: 163. 1873.

On Oncoba spinosa, Vicosa, Muller 391, Oct. 12, 1933. On dead twigs, Vicosa, Muller 708, Feb. 10, 1934.

35. Guignardia atropurpurea Chardon, sp. nov. (FIG. 26, 27, 28).

Type: Cornell Univ. Explor. Brazil 443.

Maculae amphigenae, suborbiculare, 1–5 mm. in diam., numerosis, minutis, violaceis, peritheceis compositae, sine folii discoloratione; perithecia minuta, globosa, 3–4  $\mu$  in diam., brunnea vel violacea, in mesophyllo immersa, apicis supra superficiem folii elevata, pariete brunneo pseudoparenchymato; asci clavati, 8-sporis, fasciculati, 65–75  $\times$  13–18  $\mu$ , sporis inordinatis, continuis, hyalinis, oblongo-ellipsoideis, levibus, 17–21  $\times$  7–8  $\mu$ , contextu granulato; sine paraphysibus.

Spots amphigenous, large, approximately circular, 1–5 mm. in diam., filled with numerous minute violet perithecia, but without leaf discoloration; perithecia small, .3–.4  $\mu$  in diam., brown to violet, ostiola papillate and elevated above leaf surface; wall brown, pseudoparenchymatous; asci clavate, 8-spored, in fascicle, 65–75  $\times$  13–18  $\mu$ ; spores inordinate in ascus; spores 1-celled, hyaline, long-elliptical, smooth, 17–21  $\times$  7–8  $\mu$ , context granular; paraphyses absent.

The genus Guignardia is used here in the sense of Guignardia Bidwellii (Ellis) Viala & Rav.; that is, with the concept of an uniloculate stroma with neither paraphyses nor paraphysoids and differing from Mycosphaerella only in the possession of one-celled ascospores.

On Miconia sp., Vicosa, Muller 443, Jan. 4, 1933.

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36. Guignardia punctiformis Chardon, sp. nov. (FIG. 29, 30, 31). Type: Cornell Univ. Explor. Brazil 852.

Maculae amphigenae, fere orbiculare, brunneae, 4–6 mm. in diam.; perithecia in epiphyllo, pauciora in hyphyllo, aequaliter dispersa, solitaria, in mesophyllo, subglobosa,  $145-180\times 108-160\,\mu$ ; ostiola obtusa; asci fasciculati, clavati, octo-spori,  $72-90\times 30-34\,\mu$ , breviter stipitati, apicibus .3–4  $\mu$  crassis; sporae stipatae, hyalinae, continuae, ellipsoideae vel subpyriformae,  $20-23\times 10-13\,\mu$ , leve, contextu granulato, sine paraphysibus.

Spots amphigenous, approximately circular, brownish, 4–6 mm. in diam.; perithecia conspicuous as black dots above but much less prominent below, equally dispersed, solitary, sunken in the mesophyll, subglobose,  $145-180\times108-160\mu$ , wall membrane about  $35-40\,\mu$ , thick, ostiola obtuse-papillate; asci fasciculate, clavate, 8-spored,  $72-90\times30-34\,\mu$ , short stalked, apices .3–.4  $\mu$  thick; spores crowded, hyaline, continuous, ellipsoidal to sub-pyriform,  $20-23\times10-14\,\mu$ , smooth, contents granular; without paraphyses.

On Miconia sp., Vicosa, Muller 852, Oct. 26, 1934.

37. Нертаметіл овеsa (Dur. & Mont.) Sacc. Syll. Fung. 2: 88. 1883.

On dead twigs, Vicosa, Muller 392, Jan. 12, 1933.

38. Humboldtina Bonplandi Chardon & Toro, Univ. Puerto Rico Monog. Biol. B. 2: 183. 1934.

On dead wood, Vicosa, Muller 389, Jan. 22, 1933.

39. Leptosphaeria Sacchari Breda de Haan, Med. Proefst. Suik., West-Java 1892: 25.

On Saccharum officinarum, Vicosa, Muller 301, Feb. 20, 1932.

40. Neopeckia rhodosticta (Berk. & Br.) Sacc. Syll. Fung. 11: 317. 1892.

On dead bark, Ponte Nova, Muller 257, Apr. 4, 1931.

41. Ophiobolus Cariceti (Berk. & Br.) Sacc. Syll. Fung. 2: 349. 1883.

On Oryza sativa, Vicosa, Muller 408, Mar. 20, 1933.

On Oryza sativa, Sete Lagoos, Muller 953, Jul. 12, 1935.

42. Ophiodothella Bignoniacearum Chardon, sp. nov. Type: Cornell Univ. Explor. Brazil 453.

Maculae amphigenae, conspicuae, grandes, orbicularae, brunneae, 4-10 mm. in diam.; perithecia numerosa, atro-punctiformia, amphigena, solitaria dis-

posita vel aggregata, leniter depresso-globosa, 220–300  $\times$  180–216  $\mu$ , superne clypeis et membrana prosenchymata circumdata, 6–10  $\mu$  crassa, ostiolis brevibus papilliformis, periphysibus; asci cylindracei, breviter stipitati, 8-spori, 72–85  $\times$  8–9  $\mu$ , sporis hyalinis, filiformis, continuis, stipatis, in asco; paraphyses parce evolutae, fibrosae.

Spots amphigenous, conspicuous, large, consisting of brown circular areas, 4–10 mm. in diam., provided with numerous black punctiform perithecia, visible on both surfaces of leaf; perithecia single, globose to flattened, 220–300 × 180–216  $\mu$ , with clypeus above and surrounded by prosenchymatous wall, 6–10  $\mu$ , thick, ostiole short-papillate, with periphyses; asci cylindric, 8-spored, short stalked, 72–85 × 8–9  $\mu$ ; spores filiform, hyaline, 1-celled, tightly pressed together in ascus; paraphyses present but inconspicuous with age.

This genus has all of the characters of *Linospora* Fuckel with the exception of the beak. *Ceuthocarpon* Karst. is not a synonym of *Ophiodothella*, but is synonymous with *Linospora* as its type, *C. populinum* (Pers.) Karst., also possesses beaks on the perithecia. On Bignoniaceae, Vicosa, *Muller 453*, Apr. 12, '33, and 556, May 25, 1933.

43. Ophiodothella Ingae (P. Henn.) Theissen & Sydow, Ann. Myc. 13: 614. 1915.

Vialaea Ingae Rehm, Hedwigia 40: 120. 1901.

Phyllachora Ingae P. Henn. Hedwigia 48: 8. 1908.

Scolecodothopsis Ingae Stev. Ill. Biol. Mon. 83: 183. 1923.

Diatractium Ingae H. & P. Sydow, Ann. Myc. 18: 183. 1920.

On *Inga* sp., Vicosa, *Muller 538*, May 20, 1933, and 698, Feb. 4, 1934.

44. Parodiella perisporioides (Berk. & Curt.) Speg. Anal. Soc. Ci. Argent. 9: 178. 1880.

On Crotalaria sp. Sylvestre, Muller 32, Dec. 1, 1929.

On Crotalaria sp., Vicosa, Muller 21, Nov. 14, 1929.

On Indigofera suffructicosa, Vicosa, Muller 920, May 22, 1935.

This fungus has been placed in the Perisporiaceae, but as its perithecium is in reality an uniloculate stroma with paraphysoids, it belongs along with *Apiosporina*, *Neopeckia*, *Herpotrichia*, etc.

45. PSEUDOPLEA BRIOSIANA (Poll.) Höhnel, Ann. Myc. 16: 163. 1918.

On Medicago sativa L., Machado, Muller 754, Jan. 20, 1934.

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46. PSEUDOTHIS SUBCOCCODES (Speg.) Theissen, Ann. Myc. 16: 182. 1918.

This fungus is identical with *Toro 359*, from Salgar, Colombia. The conspicuous, dirty brown pustule-like protuberances on the leaves contain numerous perithecia, with asci having brown, 2-celled spores,  $9-10.5 \times 5-6 \,\mu$ . The cells are unlike. Conidia are also found in small pockets at the borders of the fructifications. They are unicellular, brown, more or less globose,  $6-7 \,\mu$  in diameter. See figure 14, Jour. Dept. Agr. Puerto Rico 14: 270. 1930.

On Dalbergia miscolobium, Lagoa Santa, Muller 961, July 16, 1935.

On Machaerium oblongifolium, Cajury, Muller 292, Oct. 12, 1931, and Vicosa, Muller 682, Feb. 4, 1934.

On Machaerium sp., Cajury, Muller 295, Oct. 12, 1931.

47. Sphaerulina Oryzae Miyake, Bull. Coll. Agr. Tokyo Imp. Univ. 8: 245. 1910.

On Orysa sativa, Vicosa, Muller 409, Mar. 20, 1933.

48. Valsa leucostoma Pers. ex Fries, Summa Veg. Scand. 411. 1849.

On Prunus Persica, Vicosa, Muller 860, Nov. 2, 1934.

On Prunus Persica var. nucipersica Vicosa, Muller 705, Feb. 10, 1934.

#### XYLARIACEAE

49. CAMILLEA MACROMPHALA (Mont.) Cooke, Grevillea 12: 3. 1883.

On dead trunk, Vicosa, Muller 820, Jul. 2, 1934.

 CAMILLEA SAGRAEANA (Mont.) Berk. & Curt. Jour. Acad. Nat. Sci. Phila. II. 2: 285. 1853.

On dead trunk, Vicosa, Muller 18, Nov. 8, 1929.

CAMILLEA TURBINATA (Berk.) Speg. Fungi Argent. Pug. IV.,
 n. 134. 1882.

On dead trunk. Araponga, Canaan, Muller 340, Apr. 29, 1932.

52. Hypoxylon anthracodes (Fries) Mont. Ann. Sci. Nat. II. 13: 359. 1840.

On dead bark, Ponte Nova, Muller 260, Apr. 4, 1931.

53. Hypoxylon applanatum (Theissen) J. H. Miller, comb.

Nummularia commixta Rehm v. applanata Theissen, Ann. Myc. 6: 350. 1908.

The stroma is plane to convex depending on the shape of the wood, of indefinite dimensions, discrete, pulverulent, later shining black; surface is smooth with slightly raised hemispheric ostiola, widely punctate with age; ascospores fusoid-elliptical,  $25-32 \times 6-8 \mu$ .

This fungus has no connection with Nummularia commixta Rehm. The latter should bear an earlier name, Nummularia scriblita (Mont.) Cooke. It is a typical Nummularia with a circular stroma with abrupt walls, and perithecia deeply sunken in the stroma, with ostiola in cavities with wide pores and slightly raised borders. The American form, which it resembles, Hypoxylon mediterraneum (DeNot.) J. H. Miller, has more prominent strongly papillate ostiola and smaller spores.

On dead wood, Vicosa, Muller 374, Oct. 15, 1934.

- 54. Hypoxylon culmorum Cooke, Grevillea 7: 51. 1878. On Merostachys speciosa, Vicosa, Muller 817, June 9, 1934.
- 55. **Hypoxylon folicola** J. H. Miller, sp. nov. Type: *Cornell Univ. Explor. Brazil 10.*

Stromata ad superficem folii, dispersa vel aggregata, irregulariter pulvinata v. globosa, atro-brunnea, v. atria, verrucosa v. tuberculates, 1–2 mm. in diam., et .5–1 mm. alta, carbonacea; perithecia .5 mm. in diam., 2–6 in quoque stromate; ostiola colla brevi papillata v. indistincta; asci cylindracei breviter pedicellati, 8-spori, 90–120  $\times$  12–14  $\mu$ , par. spor. 70–95  $\mu$  longi; sporis oblongis v. navicularibus diluto-brunneis v. atro-brunneis, 16–20  $\times$  7–9  $\mu$ ; paraphyses praesentes.

Stromata superficial on the leaf surface, dispersed to aggregated, pulvinate to globose, dark brown varying to black in age, surface verrucose to tubercular, 1–2 mm. in diam., and .5–1 mm. high, carbonous; perithecia .5 mm. in diam., 2–6 in each stroma; ostiola necks small, papillate to indistinct; asci cylindrical, briefly stalked, 8-spored, 90–120  $\times$  12–14  $\mu$ , spore part 70–95  $\mu$  long; spores oblong to navicular, dilute brown to dark brown, 16–20  $\times$  7–9  $\mu$ ; paraphyses present.

H. verrucosum Theissen, H. megalosporum Speg., and H. umbrino-velatum Berk. & Curt. all are similar in appearance, but differ in possession of much larger ascospores.

The nearest approach is one in Kew Botanical Garden labelled *H. Kursianum* Curr. on palm and bamboo leaves. However, this is an undescribed name.

On Palmae, Vicosa, Muller 10, Oct. 17, 1929.

56. Hypoxylon truncatum (Schw. ex Fries) J. H. Miller, Trans. Brit. Myc. Soc. 17: 130. 1932.

Sphaeria truncata Schw. Syn. Car. 174. 1822.

Sphaeria truncata Schw. ex Fries, Syst. Myc. 2: 422. 1823.

Sphaeria annulata Schw. Jour. Acad. Nat. Sci. Phila. 5: 11. 1825.

Sphaeria annulata v. depressa Fries, Elench. Fung. 2: 64. 1828. Sphaeria marginata Schw. Trans. Am. Phil. Soc. II. 4: 190. 1832.

Sphaeria truncatula Schw. Trans. Am. Phil. Soc. II. 4: 210. 1832.

Hypoxylon annulatum Mont. In C. Gay, Hist. Chile Bot. 7: 445. 1850. (Excl. spec.)

Hypoxylon marginatum Berk. Outl. Brit. Fungol. 387. 1860. Rosellinia nitens Ces. Note Bot. 13: 1872.

Hypoxylon chalybeum Berk. & Br. Jour. Linn. Soc. 14: 121. 1875.

Hypoxylon glomiforme Berk. & Curt. Grevillea 4: 49. 1875 Hypoxylon Murrayi Berk. & Curt. Grevillea 4: 49. 1875.

The name truncatum is the oldest epithet and has the added validity of occurring in Systema Mycologicum. Schweinitz (Trans. Am. Phil. Soc. II. 4: 210) substituted the name truncatula for his earlier name of truncata, and (l. c. p. 190) substituted the name marginatum for his previous annulata. Types representing these names labelled by Schweinitz are in Kew Gardens, and all of them are phases of the same species.

This fungus occurs in the tropics and semitropics all over the world. There is a greenish conidial layer, followed by a very hard, black, carbonous stroma, inclosing perithecia with an annulate depression around each ostiolum. The ascospores are about  $9 \times 3 \mu$ .

The other species, H. stygium (Lév.) Sacc., has a similar ap-

pearance, but differs in smaller ascospores and in beginning as a reddish layer instead of green.

On dead bark, Vicosa, Muller 24, Nov. 15, 1929; Muller 375, Oct. 16, 1932; Muller 498, Apr. 23, 1933; Muller 707, Feb. 10, 1934.

57. Kretzschmaria cetrarioides (W. & Curt.) Sacc. Syll. Fung. 9: 567. 1891.

On dead stump, Vicosa, Muller 31, Nov. 24, 1929.

58. Penzigia enteroleuca (Speg.) J. H. Miller, comb. nov.

Hypoxylon enteroleucum Speg. Fung. Argent. 264. 1898. This fungus lies within the concept of *Pensigia* Sacc. in possessing white, woody internal tissue as in most *Xylaria* species, and in the pulvinate form of *Hypoxylon*, but with a basal constriction resembling a stipe. It differs from *Pensigia Berteri* (Mont.) Mill. in the absence of the coarse scales, and in being cupulate-depressed rather than convex. The spores in both species are about the same,  $12-14 \times 5-6 \mu$ .

On dead wood, Vicosa, Muller 42, Sept. 20, 1929.

59. Rosellinia Bresadolae Theissen var. minor Theissen, Ann. Myc. 6: 351. 1908.

On dead branches, Vicosa, Muller 494, Apr. 23, 1933.

60. Rosellinia subverruculosa Rehm, Ann. Myc. 5: 526. 1907.

On Bambusa sp., Vicosa, Muller 398, Jan. 28, 1933; and Muller 424, Mar. 24, 1933.

On Chusquea sp., Vicosa, Drummond 1118, Feb. 15, 1936.

61. Thamnomyces Chamissoni Ehr. Horae, Physic. Berol. Bonn. 79. 1820.

Xylaria Chamissonis Sacc. Syll. Fung. 1: 345. 1882.

This genus differs from *Xylaria* in the filiform-branching character of the stroma, and in the possession of single perithecia at the ends of the branches. The species is well illustrated by Moller, Phycomyceten und Ascomyceten, table 10, fig. 3, 1901.

On bark, Rio Casia, Drummond 1120, July 12, 1936.

62. XYLARIA ALLANTOIDEA Berk. Jour. Linn. Soc. 10: 380. 1869. This species differs from the common *Xylaria cubensis* Mont. in possessing more of a copper color rather than brown, and in slightly larger spores; 13–16  $\times$  5–7  $\mu$  in the former and 10  $\times$  4  $\mu$  in the latter.

On dead wood, Ponte Nova, Muller 259, Apr. 4, 1931.

- 63. XYLARIA ANISOPLEURA Mont. Syll. Crypt. 204. 1856. On dead bark, Araponga, *Drummond 902*, Apr. 19, 1935.
- 64. **Xylaria coccinea** J. H. Miller, sp. nov. Type: *Cornell Univ. Explor. Brazil 900.*

Stroma solitaria, erecta, recta, compressa, clavata, involuta,  $10\text{--}20 \times 5\text{--}8$  mm., apicibus obtusis, basi in stipitem attenuata, crusta coccinea, ostiolis atris protrudentibus, intus pallida, lignosa; stipite cylindrico, 4–5 mm. longo, 2–3 mm. crasso, atro, glabra; perithecia immersa, atria, globosa, .5 mm. in diam.; asci cylindracei, stipitati, pars, spor.  $80\text{--}110 \times 7\text{--}10~\mu$ , stipite  $30\text{--}40~\mu$  longis; octospori; sporis monostichis, cymbiformibus, continuis, fuscis,  $18\text{--}24 \times 6\text{--}8~\mu$ ; paraphyses filiformes.

Fertile stroma compressed clavate,  $10\text{--}20 \times 5\text{--}8$  mm., pellicle smooth, bright red, with black protruding ostiola, involute in age, interior pallid, woody; stipe 4–5 mm. in length and 2–3 mm. in diameter, smooth, black; perithecia immersed, globose, .5 mm. in diam.; asci cylindrical, stalked, spore part 80–110  $\times$  7–10  $\mu$ , with a stalk 30–40  $\mu$  long, 8-spored; spores uniseriate, elliptic-oblong, plano-convex, dark brown,  $18\text{--}24 \times 6\text{--}8~\mu$ ; paraphyses numerous and filiform.

This is one of the smooth forms with a bright colored pellicle, and so falls in a group with X. tabacina, and X. enterogena Mont. The spores in X. coccinea are smaller than in the former, but about the same size as those of the latter. It differs from X. enterogena in having the bright red color instead of the pale yellow of the latter.

On dead wood, Araponga, Drummond 900, Apr. 14, 1935.

- 65. XYLARIA GRAMMICA Mont. Syll. Crypt. 202. 1856. On dead wood, Vicosa, *Muller 972*, Aug. 15, 1935.
- 66. XYLARIA SCRUPOSA (Fries) Berk. Jour. Linn. Soc. Bot. 10: 382. 1869.

On dead wood, Vicosa, Muller 971, Aug. 3, 1935.

On dead wood, Vicosa, *Drummond 1034*, Feb. 15, 1936. On dead wood, Rio Casca, *Drummond 1122*, July 15, 1936.

67. XYLARIA TABACINA (Kickx) Berk. Hook. Jour. Bot. Kew Gar Misc. 6: 225. 1854.

On leaf mold, Araponga, Muller 901, Apr. 19, 1935.

#### DOTHIDEALES

68. Bagnisiopsis tijucensis Theissen & Sydow, Ann. Myc. 13: 291. 1915.

On Miconia sp., Vicosa, Muller 508, Apr. 29, 1933.

69. Coccostroma Machaerii (P. Henn.) Theissen & Sydow, Ann. Myc. 12: 269. 1914.

Phyllachora Machaerii P. Henn. Engl. Bot. Jahrb. 17: 524. 1893.

On Machaerium oblongifolium, Vicosa, Muller 179, May 29, 1930, and Muller 130, Feb. 19, 1930.

70. Dothidella tinctoria (Tul.) Sacc. Syll. Fung. 2: 627. 1883.

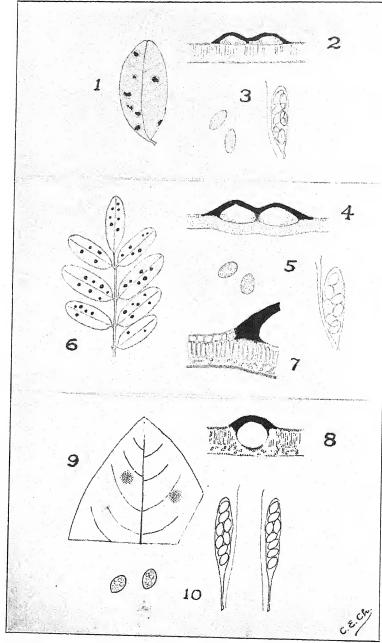
A common species on Compositae in the subtropical and temperate zones of the Andes of Colombia, Equador, and Venezuela. This is apparently the first record of the species from Brazil. The spores compare well with Colombian material. They are hyaline, 2-celled, long-elliptical,  $25-29.5 \times 9-11.5 \mu$ .

On Baccharis sp., Cajury, Muller 291, Oct. 12, 1934. On Eupatorium sp., Vicosa, Muller 999, Nov. 2, 1935.

#### PHYLLACHORACEAE

71. Catacauma copaiferiicola Chardon, sp. nov. (FIG: 1, 2, 3).

Maculae epiphyllae, ambitu, irregulari, 3–5 mm. in diam., centralibus atris nitensibus irregularibus stromatibus, 1–4 mm. diam., compositae, et flavobrunnea zona circumdatu; loculi pauci in quoque stromate, applanati, 360–400  $\times$  60–70  $\mu$ , in superiore parte crassi atri clypei et inferne nulli; asci clavati, octospori, 68–76  $\times$  13–17  $\mu$ , breviter pedicellati; sporis stipati, continuis, hyalinis, longo-ellipsoideis, apicibus acuminatis, 19–23  $\times$  8–9  $\mu$ ; contextu granulato; paraphyses praesentes, filiformes, inconspicuae.



Figs. 1-10.

Spots epiphyllous, irregular, 3–5 mm. in diam., composed of central black, shiny, irregular stromata, 1–4 mm. in diam., and a surrounding zone of yellow-brown tissue; locules few in each stroma, flattened,  $360-400 \times 60-70~\mu$ , with a thick black clypeus above and none below; asci clavate, 8-spored,  $68-76 \times 13-17~\mu$ , short stalked with spores crowded; ascospores 1-celled, hyaline, long-elliptical, with somewhat tapering ends,  $19-23 \times 8-9~\mu$ , and context granular; paraphyses filiform, inconspicuous.

This species may be synonymous with *Phyllachora Copaiferae* Speg. from Peribebuy, Brazil. However, there seem to be some marked differences between the two; Spegazzini's species has cylindrical asci,  $70\text{--}90 \times 10\text{--}12~\mu$ , and the spores are smaller,  $16\text{--}18 \times 7\text{--}8~\mu$ .

On Copaifera sp., Itabituruna, Josué Deslandes 2601, Dec. 1934. Type.

72. Catacauma hammari (P. Henn.) Theissen & Sydow, Ann. Myc. 13: 389. 1915.

On Machaerium sp., Vicosa, Muller 5, Oct. 6, 1929.

73. Catacauma mucosum (Speg.) Theissen & Sydow, Ann. Myc. 13: 373. 1915.

Phyllachora mucosa Speg. Anal. Soc. Ci. Argent. 26: 40. 1888.

The type specimen is *Balansa*, *Plantes du Paraguay 4069*, on *Cocos australis*, from Guarapi, Brazil. Our material matches well with the type. The long, graminicolous, amphigenous stromata are typical. They are shining black, well raised above the leaf sur-

Figs. 1–3. Catacauma copaiferiicola. 1, leaf of Copaifera sp. showing groups of stromata in the epiphyll; 2, cross section of leaf of Copaifera sp. showing stromatic characters of the parasite; 3, an ascus and paraphyses and two enlarged ascospores. Figs. 4–7. Catacauma Tephrosiac. 4, leaf of Tephrosia sp. showing pustular black stromata in the epiphyll; 5, an ascus, paraphyses, and two enlarged ascospores; 6, cross section of leaf of Tephrosia sp. showing the position of the stroma and locules; 7, enlarged microscopic view of fig. 6, showing details of stroma and its subepidermis position within the leaf tissues. Figs. 8–10. Phyllachora diocleicola. 8, cross section of leaf of Dioclea rufescens showing uniloculate character of the parasite and the thick heavy clypeus above the locule; 9, portion of a leaf of Dioclea rufescens showing the epiphyllous circular spots made up of many punctiform stromata; 10, two asci with long pedicels, paraphyses and two ascospores enlarged.

face. In cross-section the stromata are subepidermal, enclosing 1–3 locules. Spores are elliptical,  $18-24 \times 8-10 \,\mu$ , with a wall sometimes enclosed in a mucous sheath.

On Cocos plumosa, Vicosa, Muller 647, Dec. 7, 1933.

74. Catacauma selenospora (Speg.) Chardon, comb. nov.

Phyllachora selenospora Speg. Bol. Acad. Ci. Cordoba 11: 544. 1889.

Catacauma semilunata Chardon, Jour. Dept. Agr. P. R. 13: 7. 1921.

The Brazilian specimens show saccate asci, with eight arcuate, hyaline, 1-celled spores,  $17-19 \times 7-9 \mu$ , distinctly half-moon shaped. This spore character agrees with *Phyllachora selenospora* Speg., the type of which has been examined. It is from Apiahy, Brazil, on Myrtaceae. The spores are of the same shape,  $16-20 \times 6 \mu$ . The stromata are located between the epidermis and the mesophyll, and hence a new combination under *Catacauma* is here proposed.

Catacauma semilunata Chardon, from Maricao, P. R., seems to be the same species. Catacauma Myrciae (Lév.) Theissen & Sydow, with arcuate spores, and also on Myrtaceae may be the same, but the type has not been examined.

On Britoa rugosa, Lavras, Deslandes 2604, June 1934.

On Myrtaceae, Lagoa Santa, Muller 964, July 16, 1935.

On Myrtaceae, Curvello, Muller 1031, Mar. 1, 1936.

On Myrtaceae, Uberlandia, Muller 1079, May 17, 1936.

75. Catacauma Tephrosiae Chardon, sp. nov. (FIG. 4, 5, 6, 7). Type: Cornell Univ. Explor. Brasil 482.

Stromata epiphylla, atra, prominentia, orbicularia vel irregularia in ambitu; 1 mm. in diam., dispersa, raro confluentia, partibus foliorum maculiformiter decoloratis, inter epidermidem et mesophyllum evoluta; loculi in superiore parte stromatis clypeis compositi, inferne nulla stromata, 1–3 in quoque stromate, applanati, 250–350  $\times$  125–140  $\mu$ ; asci clavati, sporis octonis, 75–95  $\times$  21–27  $\mu$ , breviter pedicellati; sporis inordinatis vel stipatis, continuis, hyalinis, late-ellipsoideis, levis, 17–19  $\times$  8–9  $\mu$ ; paraphyses filiformes.

Stromata epiphyllous, black, prominent, circular, or irregular in outline, 1 mm. in diam., scattered, rarely coalescing, with discolored zone surrounding each stroma; stroma originating between epidermis and mesophyll, composed of heavy black clypeus above locules, with little on sides and none below; locules few, 1–3 in

each stroma, flattened,  $250-350 \times 125-140 \,\mu$ ; asci clavate, 8-spored,  $75-95 \times 21-27 \,\mu$ , short stipitate, with spores inordinate, or crowded in ascus, 1-celled, hyaline, broad elliptical, smooth,  $17-19 \times 8-9 \,\mu$ ; paraphyses filiform.

The position of the stroma in the tissue of the leaves of the host tissue is clear; it originates between the epidermis and the mesophyll, not entering the inner tissue (mesophyll). The fungus is therefore described under *Catacauma*. There is no *Phyllachora*, or like fungus attacking *Tephrosia* in the New World.

On Tephrosia sp., Vicosa, Muller 482, Apr. 21, 1933.

76. Catacauma venezuelensis (Sydow) Chardon, Jour. Dept. Agr. P. R. 16: 170. 1932.

Phyllachora venezuelensis Sydow, Ann. Myc. 28: 107. 1930.

In our specimen the stromata are epiphyllous, black, approximately circular, 1–2 mm. in diameter. The asci are saccate, 72–89  $\times$  15–17  $\mu$ , with the spores inordinate. Spores are elliptical to subglobose, 11–13  $\times$  6–8  $\mu$ , hyaline or becoming light olivaceous with age. In the type material (Sydow's *fungi exot. exs.* 830), from Puerto La Gruz, Venezuela, the spores are subglobose, 10–16.5  $\times$  9–12  $\mu$ .

On Machaerium acutifolium, Vicosa, Muller 485, Apr. 21, 1933, and Muller 289, Aug. 15, 1931.

## 77. Phyllachora Acalyphae Chardon, sp. nov.

Type: Cornell Univ. Explor. Brazil 638.

Stromata amphigena, atra, nitentia, ambitu, fere orbiculari, .5–.8  $\mu$  in diam., elevata supra superficiem folii; loculi 1–3, in mesophyllo immersi, lenticulares, magni, 340–435  $\times$  200–280  $\mu$ , clypeo crasso, atro, amphigeno et stromatibus lateraliter praesentibus; asci paraphysati, octospori, cylindracei vel cylindraceo-clavati; 73–88  $\times$  14–18, breviter pedicellati; sporae obliquae monostichae vel distichae, continuae, hyalinae, ellipsoideae, utrinque attenuatae, 14–17.5  $\times$  7–8  $\mu$ , contextu homogeneo.

Stromata amphigenous, black, shining, approximately circular, .5–.8  $\mu$  in diam., raised above the leaf surface; locules 1–3 in each stroma, in mesophyll, lenticular, large 340–435  $\times$  200–280  $\mu$ , with heavy black clypeus above and below and some stromatic tissue on sides; asci cylindrical to cylindric-clavate, 8-spored, 73–88  $\times$  14–18  $\mu$ , short pedicellate, with spores obliquely uniseriate or partially biseriate; spores hyaline, 1-celled elliptical, tapering in ends,

 $14-17.5 \times 7-8 \,\mu$ , with the contents homogenous; paraphyses present.

On Acalypha villosa, Ana Florencia, Ponte Nova, Muller 638, June 21, 1933.

### 78. Phyllachora anonicola Chardon, sp. nov.

Type: Cornell Univ. Explor. Brazil 584.

Stromata amphigena, conspicua in epiphyllo, atra, nitentia, irregulariter elevata, maculas efficientea, 1–2 mm. in diam., minus in hypophyllo visibilia, applanata, atria, opaca; loculi 1–3 vel numerosi in quoque stromate, globosi, 180–250  $\mu$  in diam., in mesophyllo immersi, clypeo crasso, atro in parte superiore, et parietibus stromaticis; asci cylindracei vel cylindracei-clavati, 93–106  $\times$  9–14  $\mu$ , octospori; sporis oblique monostichis vel sub-distichis, continuis, hyalinis, ellipsoidis, utrinque fusoidis, 12–13.5  $\times$  5–6  $\mu$ ; paraphyses praesentes.

Stromata amphigenous, conspicuous in the epiphyll, forming black shiny, irregular, slightly raised spots, 1–2 mm. in diam., less visible in the hypophyll, flat, dark, opaque; locules 1–3 or more in each stroma, globose, or nearly so, 180–250  $\mu$  in diam., located in the mesophyll with thick black clypeus above and stroma on the sides; asci cylindrical to cylindric-clavate, 93–106  $\times$  9–14  $\mu$ , 8-spored, with spores obliquely uniseriate or partially biseriate, 1-celled, hyaline, elliptical, with one end tapering, 12–13.5  $\times$  5–6  $\mu$ ; paraphyses present.

This species differs markedly, both in stromatal and spore characters, from *Phyllachora atromaculans* Sydow, on *Anona* sp., from San Jose, Costa Rica, the type of which has been examined. It differs also from *Phyllachora Anonaceae* Rehm, from Sao Francisco, Brazil, the stromata of which are "in maculis hypophyllis."

On Anona muricata, Vicosa, Muller 584, June 4, 1933.

On Anona muricata, Serra da Grama, Carangola, Drummond 916, Apr. 12, 1935.

79. Phyllachora Balansae Speg. Anal. Soc. Ci. Argent. 19:92. 1885.

The fungus appears in the form of numerous, punctiform, black stromata, covering an appreciable surface of the leaves of the host. Spores broad-elliptical,  $10-12 \times 7-9 \mu$ . A common parasite on various species of *Cedrela* in continental South America.

On Cedrela mexicana, Vicosa, Muller 669, Dec. 30, 1933.

80. Phyllachora diocleicola Chardon, sp. nov. (fig. 8, 9, 10). Type: Cornell Univ. Explor. Brazil 749.

Maculae semper epiphyllae, fere orbiculares, 4–6 mm. in diam., numerosis, minutis, atris, clypeis compositae; loculi singuli, globosi vel lenticulares, 215–265  $\times$  120–132  $\mu$ , in mesophyllo immersi, in superiore parte atri stromatici clypei, 50–60  $\mu$  crassi, supra superficiem folii, nullo stromate lateraliter et parvo inferne; asci cylindraceo-clavati, longi pedicellati, 68–81  $\times$  13–14  $\mu$ . sporis octonis; sporis monostichis vel distichis, continuis, ellipsoidis, 13–15  $\times$  7–9  $\mu$ , levibus, contextu granulato; paraphyses praesentes.

Spots epiphyllous, approximately circular, 4–6 mm. in diam., composed of numerous small black specks, the clypei of the locules; locule single, globose or lenticular, 215–265  $\times$  120–132  $\mu$ , located in the mesophyll, with heavy black clypeus above, 50–60  $\mu$  thick, which protrudes above the leaf surface, no stromatic tissue on sides and little at base; asci cylindric-clavate, long pedicillate, 68–81  $\times$  13–14  $\mu$ , 8-spored, with spores uniseriate or biseriate, 1-celled, lemon-shaped, 13–15  $\times$  7–9  $\mu$ , smooth, with context granular; paraphyses present.

The species differs from *Phyllachora Diocleae* P. Henn., reported on the same host genus from Jurua-Mity, Brazil, in macroscopic stromatal characters and in having much smaller spores. In Henning's species, the spores are elongated (langlich),  $20-23 \times 6 \mu$ . On *Dioclea rufescens*, Vicosa, *Muller 749*, Feb. 18, 1934.

81. Phyllachora chloridicola Speg. Myc. Argent. IV, n. 706. 1909.

On Chloris pycnochrix, Vicosa, Muller 27, Nov. 20, 1929.

82. Phyllachora Engleri Speg. Anal. Soc. Ci. Argent. 19: 96. 1885.

A common species in the American tropics on members of the Araceae, especially species of *Anthurium*, producing black, circular, amphigenous, spots, 2–4 mm. in diameter.

On Philodendron sp., Lagoa Grande, Muller 839, Aug. 26, 1934.

83. Phyllachora fusispora Chardon, sp. nov.

Type: Cornell Univ. Explor. Brazil 747.

Stromata amphigena, atra, linearia, prominula,  $1-2 \times .5-.8$  mm., leniter supra superficiem folii elevata; loculi 2-5 in mesophyllo immersis, applanatoglobosi vel mutua pressione angulosi,  $140-195 \times 120-145 \,\mu$ , membrana crassa atro-stromatica; asci octospori, cylindracei v. cylindraceo-clavati,  $100-130 \times 17-25 \,\mu$ , sporis magnis, monostichis v. distichis, continuis, hyalinis, longofusoideis,  $23-27 \times 6-7 \,\mu$ ; paraphyses numerosae.

Stromata amphigenous, black, linear, conspicuous,  $1\text{--}2 \times .5\text{--}.8~\mu$ , slightly raised above leaf surface; locules 2–5, flat, globose or angular through lateral pressure from others, immersed in mesophyll, black stromatic tissue on all sides,  $140\text{--}195 \times 120\text{--}145~\mu$ ; asci cylindric to cylindric-clavate, 8-spored,  $100\text{--}130 \times 17\text{--}25~\mu$ , with spores uniseriate or biseriate, continuous, hyaline, long-fusoid, large,  $23\text{--}27 \times 6\text{--}7~\mu$ , paraphyses numerous.

This species differs from all described *Phyllachorae* on *Andropogon* in the large spores and their fusoid shape.

On Andropogon sp., Vicosa, Muller 747, Feb. 18, 1934.

84. Phyllachora insularis Chardon, Jour. Dept. Agr. P. R. 13: 11. 1929.

This species is common in the West Indies and northern South America on *Valota insularis*, a host which has also gone under the name of *Trichachne insulare*. The type is from Puerto Rico, *Whotsel and Olive 551*. The stromata in the Brazilian specimen are mostly epiphyllous, black, not shiny, arranged in a row parallel to the main axis of the leaf host. The locules, which are several in each stroma, show beautifully under the microscope; asci long-cylindrical,  $72-76 \times 8 \mu$ , with the spores uniseriate, broad elliptical,  $8-9 \times 5-6 \mu$ . All these characters agree with the type material and numerous collections from the West Indies.

This appears to be the first report of the species from Brazil. The host is also new for the parasite.

On Trichachne sacchariflora, Vicosa, Muller 388, July 21, 1932.

## 85. Phyllachora Lundiae Chardon, sp. nov. (FIG. 21, 22).

Stromata minuta, punctiforma, .2-.3 mm. in diam., numerosa, atria, in utraque foliorum pagina leniter prominula; loculi singuli, globosi,  $185-220 \times 108-132 \,\mu$ , in superiore et inferiore parte atris clypeis compositi, nulli in lateribus; asci paraphysati, clavati, octospori, breviter pedicellati,  $55-65 \times 19-23 \,\mu$ , sporis continuis, hyalinis, longis, ellipticis, utrinque acutis, levis,  $18-23 \times 5-6 \,\mu$ , contextu granulato.

Stromata minute, punctiform, .2–.3 mm. in diameter, forming numerous black specks on both surfaces of leaf, slightly raised; locules single, globose,  $185-220 \times 108-132 \,\mu$ , with black clypeus above and below and none on sides; asci clavate, 8-spored, short stipitate, small,  $55-65 \times 19-23 \,\mu$ , with spores crowded in ascus, hyaline, long-elliptic with acute ends, smooth,  $18-22 \times 5-6 \,\mu$ , contents granular; paraphyses present.

This is a minute unilocular *Phyllachora* such as would fall in Spegazzini's genus *Puiggarina* (created to include the uniloculate species of *Phyllachora*). There is no evidence of a perithecial wall being present, but small black clypei are found bordering the top and bottom of the locules. Hence the fungus is retained under *Phyllachora*. The small size of the asci, their clavate shape, the crowded arrangement of the spores, and the shape of the spores are distinct specific characters of this new species.

On Lundia longa, Vicosa, Muller 464, Apr. 16, 1933.

# 86. Phyllachora mabaeicola Chardon, sp. nov. Type: Cornell Univ. Explor. Brazil 576.

Stromata amphigena fere, orbiculares, 1 mm. in diam., leniter in epiphyllo elevata; loculi 2–5 in quoque stromate, applanato-lenticulares, in mesophyllo immersi, 215–252  $\times$  132–156  $\mu$ , clypeo in superiore et in inferiore parte, lateraliter nonnullis stromaticis praesentibus; asci cylindracei, octospori, 85–94  $\times$  14–17  $\mu$ , sporis monostichis, continuis, hyalinis, globosis, 9–11  $\mu$ , membrana tenui, contextu homogeneo; paraphyses praesentes.

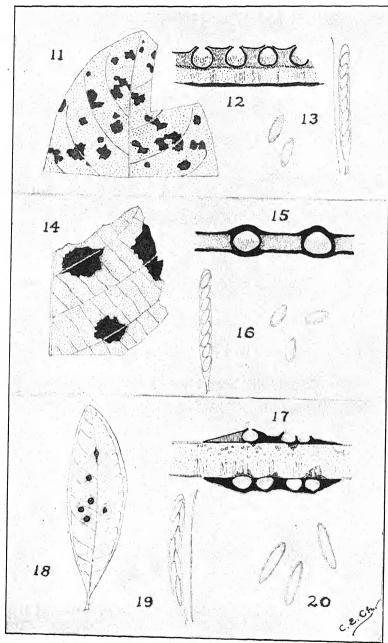
Stromata amphigenous, approximately circular, 1 mm. in diam., numerous, brown, slightly raised in epiphyll; locules 2–5 in each stroma, flat-lenticular, immersed in mesophyll, 215–252  $\times$  132–156  $\mu$ , with clypeus above and below and some on sides; asci cylindric, 8-spored, 85–94  $\times$  14–17  $\mu$ , with spores uniseriate, continuous, hyaline, globose, 9–11  $\mu$  with thin walls, contents homogenous, paraphyses present.

On Mabaea fistulifera, Vicosa, Muller 576, June 3, 1933.

# 87. Phyllachora macroloculata Chardon, sp. nov. (Fig. 11, 12, 13).

Stromata amphigena, atra, magna, conspicua, irregularia, vel angulata in ambitu, 5–8 mm. in diam., superne verrucoso-papillatis loculis, levia et atra in hypophyllo; loculi numerosi in epiphylli stromate, globosi vel subglobosi, 300–350  $\times$  240–265  $\mu$ , atris stromatibus cincta, in superiore parte tenui clypeo, stromatica membrana inter loculo, subhyalina vel dilutissime griseo-brunneolo, et stromate in hypophyllo reducto; asci longo-cylindracei, octospori, 65–78  $\times$  7–9  $\mu$ , sporis oblique distichis, continuis, hyalinis, longo-naviculare, 14–17  $\times$  5–6  $\mu$ , leves; paraphyses praesentes.

Stromata amphigenous, dull black, large, conspicuous, irregular or angular in outline, 5–8 mm. in diam., surface in epiphyll roughened with papillate locules, smooth and dull black in hypophyll; locules many in epiphyllous stromata, globose or nearly so, 300–



Figs. 11-20.

 $350 \times 240$ – $265 \,\mu$ , bordered with black stroma, with thin clypeus above and stromatic tissue between locules of much lighter color and composed of vertical elongated cells and the stroma in the hypophyll reduced to a simple, black crustlike clypeus; asci long-cylindric, 8-spored, 65– $78 \times 7$ – $9 \,\mu$ , with spores obliquely biseriate; spores continuous, hyaline, long-navicular, 14– $17 \times 5$ – $6 \,\mu$ , smooth; paraphyses present.

The stromata in this species form large, conspicuous, irregular, black spots, visible on both leaf surfaces, tar-like in appearance. The epiphyllous stromata form rather complex structures: a thin, black clypeus on the top, a black border of the individual locules and a layer of much lighter colored long cells in the interlocular region. All of these parts show very plainly under the microscope. On *Guettarda* sp., Araponga, *Muller 341*, Apr. 30, 1934.

88. Phyllachora magnificens Chardon, sp. nov. (Fig. 14, 15, 16). Type: Cornell Univ. Explor. Brazil 178.

Stromata amphigena, atra, magna, conspicua, in ambitu angularia, 1–3 cm. in diam., superne verrocosis minutibus papillatis ostiolis; maculae tenui grisea membrana circumdatae; loculi numerosi, globosi vel applanati, 265–325  $\times$  190–230  $\mu$ , crassis atris clypeis superne et inferne; asci long-cylindracei, octospori,  $105-120 \times 8-9 \mu$ , sporis oblique monostichis, continuis, hyalinis, longo-ellipsoideis, apicibus attenuatis,  $10-13 \times 5-6 \mu$ ; paraphyses filiformes.

Stromata amphigenous, black, large, conspicuous, angular in outline, 1–3 cm. in diam., surface roughened with minute papillate ostiola; spots bordered with a thin whitish tissue; locules numerous, globose or flattened,  $265-325 \times 190-230~\mu$ , with thick black clypei above and below; asci long-cylindric, 8-spored,  $105-120 \times 8-9~\mu$ , with spores obliquely uniseriate, continuous, hyaline, long-elliptical, with one end sometimes tapering,  $10-13 \times 5-6~\mu$ ; paraphyses filiform.

Figs. 11–13. Phyllachora macroloculata. 11, portion of leaf of Guettarda sp. showing conspicuous, black, irregular stromata in the epiphyll; 12, cross section of fructification showing group of epiphyllous locules and the stromatic band in the hypophyll; 13, an ascus, paraphyses, and two enlarged ascospores. Figs. 14–16. Phyllachora magnificens. 14, fragments of a leaf of Apeiba sp. showing large size of stromata; 15, cross section of leaf and stroma showing the locules and their position within the host tissue; 16, an ascus and three enlarged ascospores. Figs. 17–20. Phyllachora Mulleri. 17, cross section of leaf of Eugenia dodonaefolia showing stromata, locules and their relation with the host tissue; 18, leaf of Eugenia dodonaefolia, showing conspicuous stromata in the epiphyll; 19, an ascus and paraphysis; 20, three enlarged ascospores showing wall.

This is a handsome specimen of *Phyllachora*, with very large, black angular spots, visible on both sides of the leaves. The locules are numerous on each spot, appearing as numerous, prominent specks. The species is apparently new to science, being different from everything the writer has seen, and well deserves the specific name *magnificens*.

On Apeiba sp., Vicosa, Muller 178, May 29, 1930.

89. Phyllachora malabarensis Sydow & Butl. Ann. Myc. 9: 398. 1911.

The spores of this species are unusually large for the genus,  $27-35 \times 9-14 \,\mu$ , which do not fit any of the *Phyllachorae* described on *Bambusa* from South America. The writer has not seen the type of *malabarensis* to make a comparison, but the stromatal as well as spore characters are well within the diagnosis.

On Bambusa sp., Vicosa, Muller 113, Dec. 20, 1929.

90. Phyllachora Mulleri Chardon, sp. nov. (Fig. 17, 18, 19, 20). Type: Cornell Univ. Explor. Brazil 851.

Stromata amphigena, orbicularia vel irregularia, conspicua, atra, nitentia. 1.5–3 mm. in diam., ad superficium ob numerosos loculos papillate, zonulis violaceis cincta, in cuticulo evoluta et aetate in mesophyllum penetrantia; loculi numerosi in quoque stromate, 5–15 v. plures, globosi, apicis leniter conicis et in inferiori parte applanati,  $285-360\times218-260\,\mu$ , atro stomate circumdati; asci cylindracei vel cylindraceo-clavati, octospori,  $95-120\times13-15\,\mu$ , sporis inordinatis vel distichis, longo-fusoideis, continuis, hyalinis,  $28-32\times6-7\,\mu$ , utrinque subacutis, contextu granulato; paraphyses filiformes.

Stromata amphigenous, circular, or irregular, conspicuous, black, shiny, 1.5–3 mm. in diam., surface papillate from numerous locules, surrounded by a violet zone of host tissue; stromata originating under the cuticle and at maturity extending into the mesophyll; locules numerous in each stroma, 5–15 or more, globose, slightly conical at apex and flattened at base,  $285-360\times218-260~\mu$ , surrounded by black stroma; asci cylindric to cylindric-clavate, 8-spored,  $95-120\times13-15~\mu$ , with spores inordinate or biseriate in the ascus, spores long-fusiform, 1-celled, hyaline,  $28-32\times6-7~\mu$ , with ends sub-acute and contents granular, paraphyses filiform.

This is an interesting and beautiful species, having conspicuous, black stromata equally visible on both surfaces of the leaf. A cross section of the leaf shows the stromata with numerous locules, sub-cuticular (like a *Trabutia*), but the stromatic tissue sometimes

penetrates the inner leaf tissue, so it is described as a Phyllachora.

The spores are long fusiform, with measurements like those of *Phyllachora Petitmengini* Maire, which is known on Myrtaceae from Sao Paulo, Brazil. In stromatal characters our species seems to be very distinct. It is dedicated to its collector, the junior author.

On Eugenia dodonaefolia Teixeras, Muller 851, Oct. 26, 1934.

91. PHYLLACHORA PANICI (Rehm) Theissen & Sydow, Ann. Myc. 13: 452. 1915.

Physalospora Panici Rehm, Hedwigia 40: 114. 1901.

This species was described from the general locality of this collection. It is distinct from other species on *Panicum* in the small spores— $7-9 \times 5 \mu$ .

On Panicum sciurotes, Vicosa, Muller 489, Apr. 22, 1933.

92. Phyllachora paraguaya Speg. Anal. Soc. Ci. Argent. 19: 243. 1883.

On Luhea divaricata, Teixaras, Vicosa, Muller 2, Oct. 6, 1929. On Luhea sp., Uberlandia, Muller 1057, May 18, 1936.

93. Phyllachora Pazschkeana Sydow, Bull. Herb. Boiss. 80. 1901.

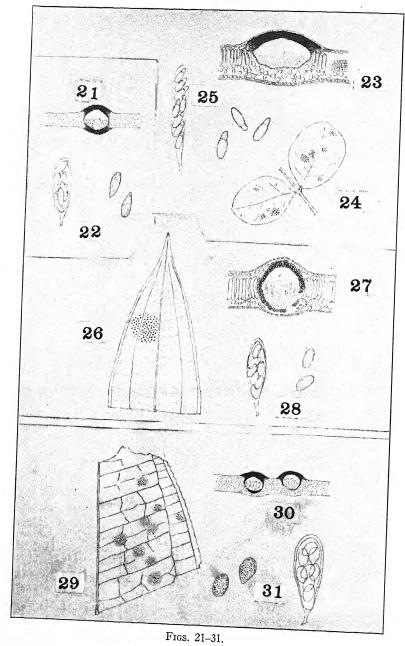
This differs from the above species on *Panicum* in possessing larger spores—10–14  $\times$  6–7  $\mu$ .

On Panicum sp., Sao Miguel, Muller 328, Mar. 19, 1932.

- 94. Phyllachora Psychotriae Rehm, Hedwigia 36: 371. 1897. On *Psychotria hancorniifolia*, Vicosa, *Muller 796*, May 20, 1934.
- 95. Phyllachora phylloplaca Chardon, sp. nov. (Fig. 35, 36, 37). Type: Cornell Univ. Explor. Brazil 491.

Maculae amphigenae, conspicuae, atria, nitentea, angulares, 3–5 mm. in diam.; loculi numerosi, minuti, 90–120  $\mu$  in diam., in mesophyllo immersi, superne atro clypeo et parvo stromate inferne; asci clavati, 8-spori, 55–63  $\times$  13–15  $\mu$ , breviter stipitati; sporis distichis vel inordinatis, hyalinis, continuis, oblongo-ellipsoideis, postice attenuatis, 9–11  $\times$  4–5  $\mu$ , levibus; paraphyses praesentes.

Spots amphigenous, conspicuous, black shiny, angular, 3–5 mm. in diam., locules many, small, 90–120  $\mu$  in diam., immersed in the mesophyll, black clypeus above and thin one below; asci clavate,



8-spored,  $55-63 \times 13-15 \mu$ , short stipitate, with spores biseriate or inordinate; spores hyaline, one-celled, long-elliptical, with one end tapering,  $9-11 \times 4-5 \mu$ , smooth; paraphyses present.

On Diclidanthera laurifolia, Vicosa, Muller 491, Apr. 22, 1933.

95. Phyllachora pusilla Sydow, Ann. Myc. 2: 163. 1904. On *Malvaceae*, Vicosa, *Muller 585*, June 4, 1933.

96. PHYLLACHORA SCLERIAE Rehm, Hedwigia 39: 232. 1900.

The type specimen is from Maua, Rio Janeiro. It has not been examined, but the material agrees well with the published description and with material from the West Indies which has been referred to *Phyllachora Scleriae*. The asci are cylindrical, with the spores biseriate. The spores long-fusiform with sub-acute ends, and the dimensions,  $21-25 \times 5-6 \mu$ , are slightly larger than Rehm's, which are  $18-22 \times 4-4.5 \mu$ .

On Scleria sp., Vicosa, Muller 427, Mar. 29, 1933.

97. PHYLLACHORA SECURIDACAE P. Henn. Hedwigia 43: 251. 1904.

On Polygalaceae, Vicosa, Muller 544, May 21, 1933.

98. Phyllachora sphaerosperma Winter, Hedwigia 21: 170. 1884.

Common throughout tropical America. Spores uniseriate or biseriate, globose,  $8-9 \mu$  in diameter.

On Cenchrus sp., Rio Branco, Muller 829, July 21, 1934.

99. Phyllachora taruma Speg. Anal. Soc. Ci. Argent. 19: 94. 1886.

On Vitex cymosa, Vicosa, Muller 166, Apr. 24, 1930.

Figs. 21–22. Phyllachora Lundiae. 21, cross section of stromata showing uniloculate character and its relation to the host tissue; 22, an ascus and two enlarged ascospores with sub-pyriform shape. Figs. 23–25. Stigmochora controversa. 23, cross section of stroma; 24, leaves of Menoxylon brauna (Muller 691) showing groups of minute stromata in the epiphyll; 25, an ascus and three enlarged ascospores. Figs. 26–28. Guignardia atropurpurea. 26, portion of leaf of Miconia sp. showing typical spot with group of perithecia; 27, cross section of perithecium with wall; 28, ascus and two enlarged ascospores. Figs. 29–31. Guignardia punctiformis. 29, a portion of leaf of Miconia sp. showing circular spots produced by the parasite, filled with minute punctiform stromata; 30, cross section of leaf of Miconia showing single perithecium with clypeus; 31, an ascus and two enlarged ascospores.

On Vitex cymosa, Maria da Fe., Minas, Muller 225, Dec. 29, 1930.

100. Phyllachora tropicalis Speg. Anal Soc. Ci. Argent. 10: 143. 1880.

The type specimen is from Cordoba, Argentine, on *Psidium Theac*. The stromata are much smaller than in the Brazilian collections, amphigenous, .5–1 mm. in diameter, embedded in the mesophyll; the spores uniseriate, elliptical,  $12-14 \times 7-8 \mu$ .

In our number 528, the stromata are much larger, only epiphyllous, black, shining, circular, raised over the surface of the leaf, 1–2 mm. across. In cross-section, microscopically, the stromata are distinctly sub-epidermal (suggestive of Catacauma) with large locules,  $500-600 \times 240-275 \,\mu$ ; asci cylindrical-clavate, the spores obliquely uniseriate or partially biseriate; spores elliptical, with blunt ends,  $15-18 \times 7-8 \,\mu$ , with the contents granular; paraphyses present.

In spite of the apparent differences between the specimen the writers do not feel justified in considering it as a new species. The material collected by the junior author compares well with *Puttemans Fungi 170*, from Serra da Cantareira, Sao Paulo, determined by Puttemans as *Phyllachora tropicalis*; also with a specimen collected by Maublanc in Bello Horizonte, Minas Geraes, which has been referred to the same species. In both of these two specimens the stromata are much larger than in the type specimen.

On Myrtaceae, Ouro Preto, Muller 528, May 2, 1933.

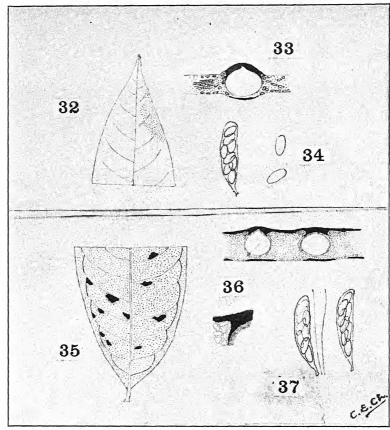
On Psidium guajava, Vicosa, Muller 823 & 824, July 11, 1934.

101. Phyllachora vernoniicola P. Henn. Hedwigia 41: 110. 1902.

On Vernonia sp., Vicosa, Muller 414, Mar. 22, 1933.

102. Phyllachora Vicosae Chardon, sp. nov. (Fig. 32, 33, 34). Type: Cornell Univ. Explor. Brazil 751.

Stromata amphigena, minuta, punctiforma, inconspicua, .2-.3 mm. in diam., sine maculis, in folii late dispersa, atra in epiphyllo, brunnea in hyphyllo; loculi singuli, globosi, vel applanati, minuti,  $125-246 \times 68-127 \mu$ , atro clypeo superne et parvo inferne; asci clavati, octospori,  $58-70 \times 12-14 \mu$ , breviter pedicillati, sporis inordinatis, hyalinis, continuis, longo-ellipsoideis, utrinque obtusis,  $12-14 \times 5 \mu$ ; paraphyses praesentes.



Figs. 32–34. Phyllachora Vicosae. 32, portion of leaf of Machaerium sp. invaded with a large number of minute stromata of the parasite; 33, cross section of leaf of Machaerium sp. showing uniloculate character of the stroma and the clypeus; 34, an ascus and two enlarged ascospores. Figs. 35–37. Phyllachora phylloplaca. 35, a portion of leaf Diclidanthera laurifolia showing typical Phyllachora-like spots of the parasite; 36, cross section of perithecia showing heavy black clypeus above and a smaller stromatic band below; 37, two asci and paraphyses.

Stromata amphigenous, small, punctiform, inconspicuous, .2–.3 mm. in diam., covering wide areas of the leaf, black in epiphyll, brown in hypophyll; locule single, globose or flattened, small,  $125-240\times68-127~\mu$ , with black clypeus above the locule and smaller one below; asci clavate, 8-spored,  $58-70\times12-14~\mu$ , short stipitate with spores inordinate; spores hyaline, one-celled, long-elliptic with ends obtuse,  $12-14\times5~\mu$ , paraphyses present.

The distinction between this species and the other on Machae-

rium, lies in the spores—12–14  $\times$  5  $\mu$  here, and 5–6  $\times$  3 $\mu$  in Phyllachora machaeriicola (P. Henn.) Th. & Sydow.

On Machaerium sp., Vicosa, Muller 751, Feb. 18, 1934.

103. Stigmochora controversa (Starb.) Theissen & Sydow, Ann. Myc. 13: 580. 1915.

Apiospora controversa Starb. Ark. Bot. 57: 22. 1905 (Fig. 23, 24, 25).

Dothidella controversa Speg. Anal. Mus. Nac. Buenos Aires 23: 95. 1912.

The stromata are punctiform, epiphyllous, black, crowded in dense groups which form spots 3–6 mm. in diameter. In cross-sections, the locules are embedded in the mesophyll, with a thick, heavy, black clypeus above and none on the sides. The asci are cylindrical-clavate, 8-spored with the spores partially biseriate in the ascus. The spores are hyaline, unequally 2-celled,  $17-19 \times 6-7 \mu$ , with the lower cell much smaller, papillate; paraphyses present.

The type specimen has not been examined, but the characters agree closely with Theissen and Sydow's description. The species seems to have a wide distribution in South America, occurring on various leguminous hosts.

On Menoxylon brauna, Vicosa, Muller 691, Feb. 4, 1934. On Tecolobium sp., Vicosa, Muller 995, Nov. 2, 1935.

104. Rhopographus Zeae Pat. Bull. Soc. Myc. Fr. 9:136. 1893. There is a linear stroma sunken in the corn culm, with a few locules in a single row, surrounded by bright colored stromatic tissue; with asci 90–130  $\times$  16–18  $\mu$ , with filiform paraphyses, and ascospores cylindric-spindle form, constricted in the middle, 35–40  $\times$  6–8  $\mu$ , 4–6 celled, brown.

On Zea mays, Vicosa, Muller 1107, Mar. 18, 1936.

105. Rнородгарния Вамвизае (Cooke) Theissen & Sydow, Ann. Myc. 13: 426. 1915.

On Bambusa pallescens, Serra da Grama, Carangola, Drummond 930, Apr. 12, 1935.

#### MICROTHYRIALES

106. ASTERINA MICONIAE Theissen, Ann. Myc. 11: 440. 1913. On *Miconia* sp., Carangola, *Muller 911*, Apr. 12, 1935.

### 107. Coscinopeltis Tetrapteridis Chardon, sp. nov.

Type: Cornell Univ. Explor. Brazil 814.

Maculae semper epiphyllae, plus-minusve orbiculares, 1.5–2.5 mm. in diam., atrae conspicuae, crustaceae, subcuticularibus stromatibus compositae; loculi numerosi in quoque stromate, applanati 400–600  $\times$  210–214  $\mu$  in superior parte clypei, inferne nulla stroma, ostiolati; asci saccati, octospori, breviter pedicellati, apicis crassis (5  $\mu$ ), et sporis biseriatis vel inordinatis, continuis, hyalinis, longe-pyriformis, utrinque arctuatis, 13–17  $\times$  4.5–6  $\mu$ ; paraphyses uncinatae, apicibus crassis.

Spots epiphyllous, more or less circular, 1.5–2.5 mm. in diam., composed of black, conspicuous, crustlike, subcuticular stromata; locules numerous in each stroma, flat,  $400-600 \times 210-214 \,\mu$ , with clypeus above and none below, ostiolate; asci saccate, 8-spored, short pedicellate, apex thick (5  $\mu$ ), and spores biseriate or inordinate; spores 1-celled hyaline, long-pyriform, with one end arcuate,  $13-17 \times 4.5-6 \,\mu$ ; paraphyses coiled and thickened at tips.

A cross-section of the fructification shows the stroma to be clearly sub-cuticular, so the fungus belongs in the tribe Munkielleae of the Polystomellaceae. In this tribe, *Coscinopeltis* has 1-celled, hyaline spores and paraphyses. Only two species have been described in this genus, from both of which our material differs widely.

On Tetrapterix sp., Vicosa, Muller 814, June 2, 1934.

## 108. Ellisiodothis Qualeae Chardon, sp. nov.

Type: Cornell Univ. Explor. Brazil 963.

Stromata hypophylla, carbonacea, tuberculata, suborbicularia, conspicua, 1–2 mm. in diam., ad superficiem folii adnata; stromata verrucosa minutissime papillata ostiolata, ad folium hypostromate centrali affixa, 120–150  $\mu$  lata, penetrans mesophyllum; loculis 2–5 in quoque stromate, sub-globosis, 225–300  $\mu$  in diam., ascis cylindraceis octosporis 90–105  $\times$  8–11  $\mu$ ; sporis oblique monostichis, continuis, hyalinis, oblongis, ellipsoideis, 8–11  $\times$  5–6  $\mu$ , utrinque attenuatis; paraphyses praesentes.

Stromata hypophyllous, carbonous, tuberculate, nearly circular, conspicuous, 1–2 mm. in diameter, closely adnate to the surface of the leaf, with surface of stroma minutely roughened with protruding ostiola, attached to leaf with central hypostroma, 120–150  $\mu$  wide, which penetrates the mesophyll; locules 2–5 in each stroma, globose or nearly so, 225–300  $\mu$  in diam.; asci cylindric, 8-spored, 90–105  $\times$  8–11  $\mu$ ; spores obliquely uniseriate, continuous, hyaline, long-elliptical, 8–11  $\times$  5–6  $\mu$ , with one end sometimes tapering; paraphyses present.

This species fits well in the genus *Ellisiodothis*, of the tribe *Polystomelleae* (which has round locules attached to the host by means of an intramatricular hypostroma). *Ellisiodothis* is the only genus in this tribe having 1-celled, hyaline spores and paraphyses.

On Qualea multiflora, Lagoa Santa, Muller 963, July 16, 1935.

109. Lembosia Melastomatum Mont. Ann. Sci. Nat. IV. 5: 373. 1856.

On Miconia Mendoncaei, Vicosa, Muller 580, June 2, 1933.

110. Echidnodes Baccharidincola (Rehm) Theissen & Sydow, Ann. Myc. 15: 422. 1917.

On Baccharis sp., Ouro Preto, Muller 529, May 2, 1933.

111. Rhagadolonium Cucurbitacearum (Rehm) Theissen & Sydow, Ann. Myc. 12: 275. 1914.

On Cayaponia sp., Vicosa, Muller 305, Mar. 5, 1932.

#### HELOTIALES

112. DISCOHAINESIA OENOTHERAE (Cooke & Ellis) Nannf. Nova Acta Reg. Soc. Sci. Upsal. IV. 8: 88. 1932.

Pesiza Oenotherae Cooke & Ellis Grevillea 6:90. 1878.

None of the many different names applied to this fungus, such as *Pezisella Lythri* (Desm.) Shear & Dodge, are correct because they are based on a conidial stage.

On Fragaria chiloensis, Vicosa, Muller 242, Feb. 26, 1931.

113. Phaeofabraea Miconiae Rehm, Ann. Myc. 7: 541. 1909. This discomycete is a parasite on the stroma of Bagnisiopsis tijucensis Theissen & Sydow. The spores are brown, 2-celled, 10–14 × 6–7 μ. The type was collected in Sao Leopoldo, Brazil. On Miconia Candolleana, Vicosa, Muller 606, June 6, 1933.

#### TAPHRINALES

114. Taphrina deformans (Berk.) Tul. Ann. Sci. Nat. V. 5: 122–236. 1866.

On Prunus Persica, Itajube, Muller 1133, Oct. 15, 1936.

## STUDIES ON TWO STRAINS OF APHANO-MYCES LAEVIS FOUND OCCURRING AS WOUND PARASITES ON CRAYFISH <sup>1</sup>

RALPH I. SMITH <sup>2</sup> (WITH 1 FIGURE)

During 1937 and 1938 a number of young crayfish (Cambarus Clarkii Girard) which had recently been operated upon in these laboratories 3 died, apparently as the result of infection with a water mould which after isolation was tentatively identified as Aphanomyces laevis De Bary. Since this species is not very clearly defined, and has never been reported as parasitic upon animals, and because of the fact that a severe, recurring epidemic disease of European crayfish is caused by a species of Aphanomyces (A. astaci = magnusi Schikora), which is, however, quite different from A. laevis, the following studies were made to determine more carefully the morphology, development, and taxonomic position of the present fungus.

Two strains, A and B, believed to be A. laevis have been isolated, each from a different lot of crayfish. These isolates, although morphologically very similar, show important physiological differences which are of interest in view of the varying descriptions of A. laevis that have previously been given.

The hyphae of both strains are slender and whitish, rather straight, with occasional side branches given off nearly at right

- <sup>1</sup> Contribution No. 180 from the Laboratories of Cryptogamic Botany and the Farlow Herbarium, Harvard University.
- <sup>2</sup> I am greatly indebted to Miss P. F. Sullivan and Dr. John R. Raper for their kind help in the preliminary isolation and identification of the fungus here discussed. To Dr. W. H. Weston, Jr., under whose direction the body of this work has been done, I am especially grateful for much advice and encouragement.
- <sup>3</sup> The geographical source of the fungus to be discussed is not known. The crayfish infected with it were hatched at Cambridge, Massachusetts, from the eggs of crayfish shipped from Louisiana, but were kept for a time in tanks previously occupied by animals from other distant areas.

angles to the main axis. The diameter of hyphae grown on Difco cornmeal agar is from  $3.5~\mu$  to  $8.5~\mu$ , averaging  $6~\mu$ . The hyphae taper only slightly, the tips being bluntly rounded. The mycelial growth of both strains on most types of nutrient agar is submerged and similar, the radial growth rate of both on Difco cornmeal agar, for example, being about  $0.9~\rm cm$ . per day at room temperature. However, on unstrained cornmeal agar, strain A shows a sparse aerial growth, while strain B develops an aerial growth sufficiently dense to conceal the substrate.

Asexual reproduction in both strains is typical of the genus. The sporangia appear to be undifferentiated hyphae, sometimes branched, delimited proximally by a hyaline plug. The encysted zoöspores are  $8-11.5 \mu$  in diameter, remaining in clusters at the mouths of the long sporangia. Zoöspores are often left in the sporangium as cylindrical bodies of various lengths which may germinate in situ. Especially in old cultures, there is a pronounced tendency for the hyphal contents to aggregate to more or less elongate, sometimes branched, bodies which can sprout when placed in fresh water. When pieces of old agar cultures are placed in fresh water, slender sporangia form, which discharge small masses of 6-20 encysted spores. Larger sporeballs, such as are common in the genus, containing 100 or more spores, are usually produced by strain B when it is grown on hempseed in water, but almost never by strain A. The encysted primary zoöspores may germinate directly, or may release laterally biflagellate secondary zoospores which settle down and develop, usually by unequal bipolar germination.

Sexual reproduction is by means of antheridia and oögonia, which in strain A are formed rapidly and in great numbers on hempseed in water and on unstrained cornmeal agar, but never on Difco cornmeal agar. Strain B, on the other hand, forms oögonia only very rarely under any conditions. The oögonia of the two strains cannot be distinguished from each other, either in size or in general appearance (Fig. 1). In its scanty and slow production of oögonia, strain B is very similar to Coker's (1) typical form of A. laevis, but the rapid and abundant production of oögonia by strain A marks it as different from Coker's typical form in this respect.

Oögonia are formed singly or in small clusters, antheridial branches investing them in a loose tangle in which the connections are largely obscured. The antheridia appear to be of diclinous origin, but because most oögonia are formed on cloudy or opaque solid media it cannot be stated that these strains are invariably diclinous. The oögonial stalk sometimes winds closely about an antheridial branch, a condition reported by Drechsler (3) for A. cladogamus and A. camptostylus.

The oögonia are globose, 20– $35~\mu$ , averaging  $28~\mu$ , in diameter, with a smooth hyaline wall about  $\frac{3}{4}~\mu$  thick. Because of the refractive nature of this wall, it is difficult to measure in optical section, but many observations have led to the conclusion that it is of uniform thickness, without the sinuous inner contour found in several species of *Aphanomyces* occurring as root parasites (Drechsler, 3). The septum of the oögonial stalk is seldom observed because of the intertwining of the oögonial and antheridial branches. In all cases in which the septum has been seen, it has been found to lie not at the point where the stalk meets the globe of the oögonium, but at a distance usually as great as or greater than the radius of the globe (FIG. 1).

The single round oöspore is  $16-29 \mu$  in diameter, averaging  $22 \mu$ , with a smooth, non-refractive wall about  $1 \mu$  thick, which in any given oögonium is almost always thicker than the oögonial wall.

The oöspore wall is not quite hyaline, having a faint brownish or purplish tinge. The content of the oöspore is yellow-brown to olive with a regularly granular peripheral cytoplasm enclosing a large, slightly eccentric oil-drop. A small, clear vesicle is usually found lying in the thickest part of the granular area (FIG. 1). There is a tendency for the oögonia to be slightly larger when grown on solid nutrient agar than when developed on hempseed in water, but the appearance is very similar in all cases.

A feature which is not satisfactorily measured, but which is of taxonomic importance is the form of the antheridium. In my isolates there are one to three antheridia per oögonium, of the shape typical for A. laevis, that is, elongate, rather vermiform and constricted at intervals so as to rest upon the oögonium at several points like stout caterpillars (FIG. 1). The diameter increases gradually from the septum, the extreme end being bluntly rounded.

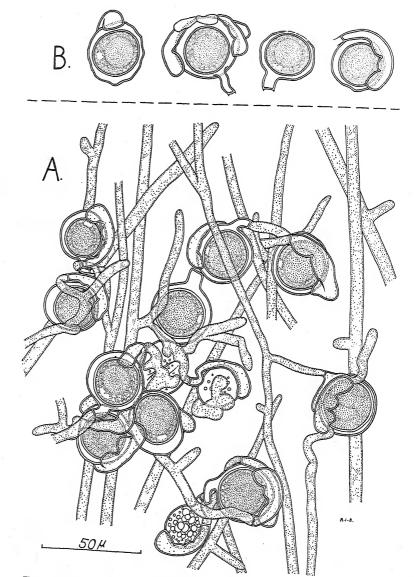


Fig. 1. The sexual organs of *Aphanomyces lacvis*, grown in unstrained cornmeal agar cultures and drawn in the living condition with the aid of a camera lucida, at an original magnification of  $1000 \times$ . The present magnification is about  $550 \times$ , the exact measurements being shown in the scale, which applies to both (A) and (B). A. Oogonia, oospores, antheridia, and hyphae of strain A, drawn in situ, slightly simplified. The abundant for-

The antheridia differ, therefore, from the short, globose antheridia, or those with apical prolongations such as are found in the several soil inhabiting *Aphanomyces* figured by Drechsler (3).

That strain A is not homogeneous is indicated by the fact that from this strain cultural lines have been derived which produce no oögonia, but until further work has been done, no explanation can be offered. Of two single-spore lines of strain A, one has produced oögonia, the other has not.

The ability of strains A and B to infect wounded crayfish is probably not greatly different. All the animals naturally infected with strain A died, but attempts to inoculate healthy crayfish with it gave such indefinite results that I decided it was merely a wound parasite which could bring about the death of a weakened animal by preventing wound healing and increasing the chance of further infection by other organisms. Strain B showed little tendency to spread from animal to animal and was usually not fatal, but this lack of virulence may be attributed as much to the excellent health of the crayfish at that time and the prompt attempts to check the spread of the infection as to any lesser degree of infectiousness in this strain.

The appearance of the sexual organs (FIG. 1), and the measurements summed up in table I make it clear that both strains A and B can be assigned to the species *Aphanomyces laevis*. Several previously published measurements of this species, also included in table I, show that the species, as defined in the literature, is somewhat variable. A few words of explanation regarding several points in the table are necessary. As De Bary's (2) measurements are given in lines ( $\frac{1}{12}$  inch;  $\frac{1}{12}$ ), the values marked with an asterisk are taken from Peters (7), who converted De Bary's values into micra. The value marked with a ( $\frac{1}{12}$ ) for diameter of oögonia after De Bary is Coker's (1) conversion of De Bary's measurements. Coker states that this is De Bary's neasurement of the "eggs" of *A. lacvis*, but as De Bary gives values only for

mation of sexual organs is characteristic of this strain. B. Several oogonia, oospores, and antheridia of strain B. These are rarely formed, but may be seen to be in all respects similar to those of strain A.

TABLE I

THE CHARACTERISTICS OF A. Ideevs and A. asfaci, Taken from Several Previous Authors for Comparison with those of the Strains Discussed in this Paper

)		MYCOI	JOGIA,	VOL.	02, 1940	J		
Antheridia	Elongate, rather lobed, androgy-nous or diclinous	Abundant, cylindrical, lobed, androgynous or diclinous	Elongate		Elongate, vermi- form, diclinous	Elongate, vermi- form, diclinous		Androgynous, not always present
Oöspore wall	I	‡"Thick"		‡3–5(6)μ	0.5–1.5 $\mu$ av. 1 $\mu$	$0.5-1.5\mu$ av. $1\mu$		-
Oögonial wall Oöspore wall	Thin, smooth	Thin, smooth	Smooth, sinuous	up to $1.5\mu$	$0.5-1\mu \text{ av. } 0.7\mu$	0.5-1 $\mu$ av. 0.7 $\mu$		22.4–28.8µ "Feinstach- eliger, hyaline"
Diameter of oöspores		16.5–26μ	$14-19\mu$	$14-22.1\mu$	$16-29\mu$ av. 22.5 $\mu$	19–24 $\mu$ av. 21.5 $\mu$		22.4–28.8µ
Diameter of oögonia	*26.3-31.4\(\pi\)	18–33μ	$22-32\mu$	$8-10.8\mu$ 18.7-25.5 $\mu$	8–11.5µ 20.5–35µ av. 28µ	22.5–29 $\mu$ av. 26.9 $\mu$		41.6–48μ
Diameter of encysted zoöspores	*9.7μ	7.3–11μ	$8.5-10\mu$	$8-10.8\mu$	$8-11.5\mu$	$8-11.5\mu$	$13\mu$	$8.1-9.5\mu$
Diameter of sporangia	*6.5µ	Same as 7.3–11 $\mu$ hyphae	3-6.6 $\mu$ Typical 8.5-10 $\mu$		Same as hyphae	Same as hyphae	$10\mu$	Same as $8.1-9.5\mu$ hyphae
Diameter of hyphae	*5.3µ	$5-7.5\mu$	$3-6.6\mu$	$5-9(10)\mu$	3.5-8.5µ av. 6µ	4-8.5μ av. 6μ	$10\mu$	7.5-9.5µ
Occurrence	Dead insects in water	Saprophytic	Parasitic on desmids and diatoms	Parasitic on beets	Wound parasite on crayfish	Wound parasite on crayfish	Severe parasite of European crayfish	Severe parasite of European crayfish
Worker	De Bary (2)	Coker (1)	Coker (1)	Peters (7)	Smith (this paper)	Smith (this paper)	Schikora (12)	Renner- felt (9)
Species	A. laevis	A. laevis	A. laevis	A. laevis	A. laevis (strain A)	A. laevis (strain B)	A. astaci Schikora (12)	A. astaci

the oögonia, I believe Coker was referring to oögonia, not to "eggs" or oöspores. Measurements of De Bary's (2) plates show that De Bary probably used the French "ligne" (line) equal to 2.256 mm. My reconversion of De Bary's values gives the size of oögonia in A. laevis as 26.2-31.3 μ, thus agreeing more closely with Peters' conversion than with Coker's. The thick oöspore walls reported by Peters (7) in his form of A. laevis parasitic on beets, and likewise by Coker for his typical form, are probably caused by the onset of degeneration in the oöspore as suggested by Drechsler (3). I have observed that application of glycerine or lactophenol will cause an oöspore wall to swell, in a few seconds, to several times its normal thickness, thus rendering preserved material unsuitable for measuring. From the above considerations, it may be seen that there are no serious discrepancies between the measurements I have given for my isolates and the values previously reported by several other workers for A. laevis. With the identity of my isolates established on morphological grounds, it is of interest to compare their physiological traits with those reported by other workers for A. astaci and A. laevis.

Since my isolates were obtained from crayfish, a survey was made of the literature on the European crayfish disease (Krebspest), which is caused by Aphanomyces astaci (= magnusi) Schikora. This disease, which first swept through Europe in the 1860's and 70's, has been discussed at length by Schikora (11, 12), Schäperclaus (10), Nybelin (5, 6), Rennerfelt (9), and a number of others. Although some of the data are contradictory, the measurements summarized in table I show that A. astaci differs from A. laevis not only in the size of its hyphae and oögonia, but also in the surface of the oögonial wall, which in A. astaci is not smooth but finely prickly. A further point, not in itself conclusive, is that A. astaci is restricted to the European crayfish Potamobius (= Astacus) and does not attack the introduced American species Cambarus affinis Say (Schäperclaus, 10). Thus it is evident that although the present fungus has been found on crayfish, it is not the same fungus that causes the European crayfish disease.

A survey of the host range of A. laevis reveals a rather great variation among the types reported by several workers. De Bary

(2) described A. laevis from Germany as occurring on dead insects in water. Coker (1) in the United States finds it typically saprophytic, but describes a variety as parasitic upon desmids and diatoms. In addition, A. laevis has long been considered as contributing to the root rot (Wurzelbrand) of sugar beets in Europe (Peters, 7), although this identification has been questioned by Drechsler (3). Finally, my isolates have been obtained from crayfish, but have been found to grow very well saprophytically on plant or animal material. In view of Peters' (7) findings, I have made several attempts to infect pea and beet seedlings with my isolates, but to date have observed no damping-off. However, as Peters (8) reports that A. laevis is responsible for only about 11 per cent of the observed cases of root-rot of beets, it cannot be considered a particularly active parasite, and my failure to obtain infection is neither surprising nor significant. From the above considerations it is apparent that the several physiological descriptions of A. laevis are not in agreement. This disagreement may well be the reflection of a real variability in nature, a variability strikingly shown in the reproductive habits of the two morphologically similar strains of A. laevis described in this paper.

The genus Aphanomyces is strongly inclined to be parasitic upon animals (Gicklhorn, 4) as well as on the higher plants (Peters, 7; Drechsler, 3) and the lower plants (Coker, 1), while generally able to exist saprophytically in culture or on plant or animal remains. The fungus which has been dealt with in this paper exemplifies well the mild facultative parasitism which may in other forms have led to true parasitism. For reasons stated earlier, the present isolates are considered merely wound parasites whose mild nature makes it unlikely that they can be dangerous pests except where crayfish are kept under crowded and unhealthful conditions.

#### SUMMARY

- 1. Aphanomyces laevis De Bary has been found occurring as a mild, facultative parasite in the wounds of young crayfish (Cambarus Clarkii) kept in the laboratory.
- 2. Two morphologically similar strains are described, one of which produces few zoöspores and many oögonia, the other of which forms few oögonia but many zoöspores.

3. In identifying these strains as *Aphanomyces laevis*, the physiological variability of the species as reported by previous authors is considered. In view of this variability, the differences in the reproductive habits of the two morphologically similar isolates discussed in this paper are of interest.

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## CONTRIBUTIONS TO THE LIFE HISTORY OF A SYSTEMIC FUNGOUS PARASITE, CRYPTOMYCINA PTERIDIS <sup>1</sup>

SARA BACHE-WIIG <sup>2</sup> (WITH 26 FIGURES)

A disease of bracken <sup>3</sup> (brake) caused by *Cryptomycina Pteridis* (Rebentisch ex Fries) von Höhnel is wide-spread in America as well as in Europe and occurs also in northern Asia. The disease has been called "leaf roll" (Killian, 1918) and is characterized by curling and stiffness of the pinnules of young fronds, accompanied by yellowish-green discoloration and the appearance of brown spots and of abundant black stromatic areas on the lower surface of the pinnules between the veinlets (FIGS. 2, 3). These areas resemble the sori of an *Asplenium*, as observed by Rebentisch (1804). Formation of conidial fructifications during the

<sup>1</sup> A thesis presented to the faculty of the Graduate School of Cornell University in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

<sup>2</sup> The writer gratefully acknowledges the valuable advice and criticism received from Professor H. M. Fitzpatrick during the progress under his direction of these studies.

She is also indebted to Professor H. H. Whetzel for encouragement and for aid in securing materials, to Professor A. J. Eames for help in interpreting the structure of the bracken, to Professor L. Knudson for directions for growing bracken in culture, and to Professor L. M. Massey and Professor Frances Grace Smith for critical reading of the manuscript.

<sup>3</sup> Since the bracken, which, under the name *Pteridium aquilinum* (L.) Kuhn (= *Pteris aquilina* L.), has been considered the most cosmopolitan of ferns (Christ, 1910), is now treated as several species, it should be made clear that the species used in the observations and experiments reported on in this paper is the eastern bracken, the *Pteridium latiusculum* (Desv.) Hieron. ex R. E. Fries of Broun's "Index to North American Ferns" (1938), while the Eurasian species, host of the fungus studied by Killian (1918), is, according to the same authority, *Pteridium aquilinum* (L.) Kuhn, represented in America by the variety *P. aquilinum lanuginosum* (Boug.) Fernald of western North America, the Great Lake region and eastern and southern Quebec. A third North American species is *Pteridium caudatum* (L.) Maxon, found from Florida to Louisiana and southward.

growing season is followed by the development of stromata in which asci mature the following spring.

Photographs of diseased and healthy fronds and pinnules, and a series of excellent drawings of the development of acervuli and ascus fructifications <sup>4</sup> illustrate the account which Killian (1918) gives of the disease. Mains (1935) gives a good photograph of overwintered, mature ascus fructifications.

Further consideration of the disease will be prefaced by (1) a brief description of the morphology of the host, and (2) a consideration of the fruiting structures of the parasite.

#### THE HOST. MORPHOLOGY

The bracken has a stout, black, creeping underground stem rounded above and below, with a narrow ridge along each side. "The young plant starts as a single axis bearing 7 to 9 alternating leaves, spirally arranged, after which it undergoes distal and equal dichotomy. . . . The two branches burrow downwards into the soil, bearing leaves alternately right and left; in the later phases of their development they also show dichotomies, but with unequal shanks: . . ." (Bower, 1923).

The rhizome tips and the very young leaves, which will hereafter be called stem buds and frond buds, respectively, are lighter in color than the mature rhizome. They can be distinguished from each other by their orientation and form: the stem buds are straight and usually horizontal, while the frond buds are vertical, and bent or coiled at the tip.

The fronds of the bracken grow singly from the rhizome. The first coiled young fronds or crosiers appear above ground in May, unrolling and maturing progressively from base to tip, in the manner characteristic of ferns.

Cross sections of the rhizome show that a band of cortical sclerenchyma forms a hard outer rind, broken only by the two ridges

<sup>4</sup> The author has found no report of the occurrence of the perfect stage of *Cryptomycina Pteridis* on any hosts other than species of bracken. The imperfect stage, however, under the name *Fusidium Pteridis*, has been reported on three other ferns: in Europe on *Phegopteris* by von Thümen and by Voss (Lindau, 1907), and on *Aspidium spinulosum* by von Thümen (Lindau, 1907); and in the United States on *Aspidium marginale* by Trelease (1884).

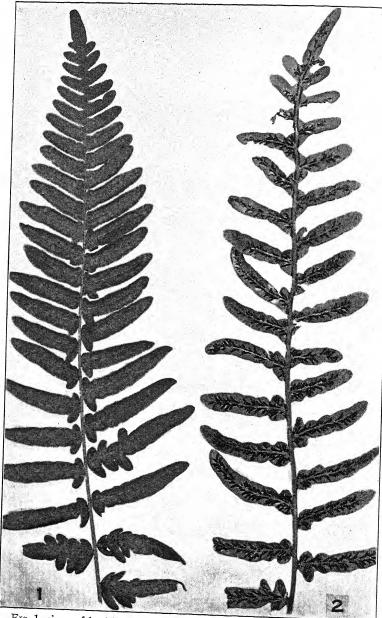


Fig. 1, pinna of healthy bracken; 2, pinna of diseased bracken, systemically infected with *Cryptomycina Pteridis*. Figs. reduced 1/4. (Photograph by Mr. W. R. Fisher.)

already mentioned, in which "... the sclerenchyma is replaced by highly ventilated parenchyma ..." (Bower, 1923). Strips of sclerenchyma are present also near the center of the rhizome, where they separate an inner series of vascular strands from an outer series, both imbedded in parenchyma. Each strand is made up of an encircling endodermis, very conspicuous because of the browning of its cell walls, below which lies pericycle, followed by sieve tubes and next by thick-walled tracheids and vessels which occupy the center of the strand. Parenchyma cells are found in both the xylem and the phloem (Bower, 1923).

A median longitudinal section of a stem bud (FIG. 8) shows that the rhizome tip is slightly concave, and that the depressed embryonic region is protected by hairs. At the bottom of the depression lies the large apical cell. The cells adjacent to the apical cell are also large, but farther away, as a result of repeated cell division, they are much smaller. Differentiation of tissues takes place a very short distance behind the meristematic tip.

A stipe (petiole) in cross section differs in outline from a rhizome, being flattened to concave on the anterior side, except at the base. Its tissues, including ventilating tissue, are essentially the same as those of the rhizome. Although the frond receives vascular strands from both the inner and outer series of the rhizome (Bower, 1928), their arrangement is not maintained in the stipe, and the sclerenchyma, instead of forming a broken band, has the form of a T or a Y.

A median longitudinal section of a frond bud shows the developing lamina (blade). In very young buds this is a simple curved process of undifferentiated cells; in older buds, pinnae are visible as lobes of the process.

#### THE PARASITE. FRUITING STRUCTURES AND TAXONOMIC POSITION

The perfect stage of the fungus was first seen by Fuckel (1869), who describes the asci as sessile, 8-spored,  $64 \times 14 \mu$ , and the ascospores as subdistichate, perfectly oval, one-celled,<sup>5</sup> mostly biguttulate, hyaline,  $8 \times 6 \mu$ . A more complete description is given

<sup>5</sup> The description of the ascospores as elongated and triseptate, given by Cooke (1871), is obviously based on the examination of the asci of some other fungus occurring in company with *C. Pteridis*.

by Starbäck (1889), who observed that the ascospores might be distichate, transversely monostichate, or crowded in the upper part of the ascus, and that while most of the spores are ovoid, some are ellipsoidal and some even round, measuring  $8.5-12~\mu \times 5-6.5~\mu$ , most often  $10.5 \times 6~\mu$ , the globose ones  $7.5~\mu$ . This variation in arrangement, form, and size of ascospores agrees entirely with observations on material collected at Ashfield, Mass., in June, 1939, by the present investigator. Absence of paraphyses is mentioned by several authors (Saccardo, 1883; Karsten, 1885; Starbäck, 1889), while Rehm (1896) first records their presence and describes them as filiform, very sparse; and delicate. Filaments of this description are present in the materal from Ashfield but since they evidently are remains of an interthecial stroma they are not true paraphyses but paraphysoids, in the sense in which the terms are used by Gäumann and Dodge (1928).

The asci are borne in a flat layer in apothecium-like, subepidermal fructifications having an upper covering as well as a basal part, both characterized by vertically arranged cells with dark, thickened walls (Killian, 1918). As emphasized by Nannfeldt (1932), the investigations of Killian prove the purely stromatic origin of the plectenchyma which encloses the ascus layer, since it is formed from an originally compact tissue, the cells of which become loosened and absorbed as the asci develop. This fruit body, which lacks a true apothecial envelope as defined by Nannfeldt (1932), will be referred to in this paper as a "pseudothecium," following the usage of Nannfeldt. When dead infested fronds overwintered on the ground become soaked by spring rains, the covering of the pseudothecium becomes irregularly torn, exposing the asci from which spores begin to be shed at about the time the first bracken fronds are unrolling. For several weeks ascospores continue to be freed after rains (Killian, 1918).

Recognizing the dothideoid structure of the pseudothecium of this fungus, Fuckel (1869) placed it in the genus *Phyllachora* <sup>6</sup> Nitschke, of the Dothideaceae Nitsch. It was transferred by Rehm (1896) to the Phacidiaceae and placed in the genus *Cryptomyces* erected by Greville (1826) on the willow parasite *Crypto-myces* erected.

<sup>&</sup>lt;sup>6</sup> For the synonymy of the perfect stage of the fungus see Oudemans (1919).

myces maximus (Fries) Rehm, which forms massive subperidermal ascus fructifications on the branches of its host, becoming erumpent at maturity and exposing the flat ascus layer by irregular dehiscence of its covering. Von Höhnel (1917) removed the bracken parasite from the genus Cryptomyces Grev. and made it the type of a new genus, Cryptomycina v. Höhn., because its fruit body is sub-epidermal instead of sub-peridermal. And since the position of the fruit body in relation to the substratum is the basic character for von Höhnel's delimitation of families within the Phacidiales, the two genera are placed in different families, Cryptomyces in the Cryptomycetaceae and Cryptomycina in the Phacidiaceae. (The statement by Gäumann and Dodge (1928) that the bracken parasite belongs to the Cryptomycetaceae of von Höhnel's treatment is based upon the assumption that the fungus conforms to the genus *Cryptomyces* Grev. as limited by you Höhnel, whereas he expressly makes this fungus the type of the genus Cryptomycina v. Höhn.) Whatever criticisms may be leveled at von Höhnel's treatment of the Phacidiales (e.g. Petrak, 1924; Nannfeldt, 1932) his separation of Cryptomycina v. Höhn. from Cryptomyces Grev. is upheld by the recent investigations of Nannfeldt (1932) who shows that the massive fruit body of Cryptomyces maximus has a distinctive four-layered structure. A basal layer of loosely woven, hyaline hyphae is followed by a wider, more compact layer showing thick, faintly colored walls, while a third, narrow layer is made up of cells with very thick, dark walls, forming a compact, sharply delimited tissue toward the outside where it gives place to the fourth layer, a compact palisade-like tissue of straight, parallel, perpendicular, hyaline, thinwalled septate hyphae. The asci develop in this outer layer. more delicate fruit body of Cryptomycina Pteridis has a different, far more simple structure. As described by Killian (1918), it consists of a compact plectenchyma of isodiametric cells with thick, brown walls, surrounding a central layer of hyaline, thin-walled, perpendicularly elongated cells. The asci develop in the central layer. In the light of the two investigations just cited, Nannfeldt (1932) considers both genera to have purely stromatic fructifications (pseudothecia), and he therefore places them not in the Phacidiaceae of his Ascohymeniales, but in the Pseudosphaeriales of his Ascoloculares.

The conidia of Cryptomycina Pteridis were first described as Fusidium Pteridis by Kalchbrenner (1861), who considered them to be those of another fungus growing in company with C. Pteridis (called by Kalchbrenner Dothidea Pteridis Fries). As described by him the conidia are cylindrical, straight or slightly curved, blunt at both ends, hyaline. Six years earlier, however, Strauss (1855) had published a general description of the development of Dothidea Pteridis including observations on the formation of the conidial fructifications, described as vesicles with milky contents of "... unzählige weisse walzige Körperchen (Spermatien)." The description was not amplified, and Fuckel (1869) is credited with being the first to consider that these spores represent the conidial stage of C. Pteridis, called by him Phyllachora Pteridis (Rebent.) Fuckel. Killian (1918) has conclusively proved that the asci and the conidia belong to the same fungus. In addition to showing the successive development and basic structural similarity of the two kinds of fructifications, he has described cases in which one half was producing conidia while the other half of the same structure was developing into an ascus fructification. This has been observed also by the present investigator in material from Ashfield, Mass.

It is interesting that the first recorded measurements of the conidia were not made in Europe but in America, by Peck (1875), who gives the length of the conidia as .0004–.0005 inch. Expressed as 10–12 microns these measurements are quoted by Karsten (1885), and he, in turn, is quoted by Rehm (1896). Later investigators have found that both larger and smaller conidia occur. Bubák and Kabát (1906) give the dimensions as 9–13  $\mu \times 2.5-4 \mu$ , while von Höhnel (1925) gives 9–16  $\mu \times 2-4.5 \mu$ . Typical conidia from diseased fronds in the Smith College Plant House ("descendants" of material collected at Ashfield, Mass.), measured at different times by the present investigator, varied within the limits 7–16  $\mu \times 3.5$ –5.5  $\mu$ . Material from Ringwood, near Ithaca, N. Y., measured 10–16  $\mu \times 4$ –5  $\mu$ . Occasionally a much larger conidium could be found, up to 23  $\mu$  in length.

Measurements by several American investigators, including

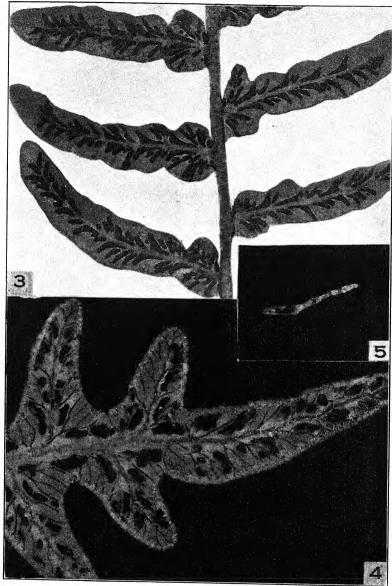


Fig. 3, pinnules of systemically diseased bracken, × 2, showing intercostal stromata of *Cryptomycina Pteridis*; 4, tip of younger diseased pinna, × 8, with whitish droplets of conidial ooze on dark areas; 5, germinating conidium in dark-field illumination, × 510. (Photographs by Mr. W. R. Fisher.)

Davis (1924) and Gilman and Archer (1929), have been purposely left out, because the present writer is not yet ready to accept either the extensive synonymy of Gilman and Archer (1929) or a more limited one such as that of Davis (1924).<sup>7</sup>

As noted by Kalchbrenner (1861), Peck (1875), and others, the conidia are held together in a sticky mass as they are forced out of the conidial fructifications, and may form little whitish to amber globules on the surface of the dark spots (FIG. 4). Sometimes they are forced out as cirrhi. It is evident that the conidia are not borne by air currents but by water.

The fructifications from which these conidial masses ooze have been described by Killian (1918) as follows. At first they are small structures with a loose basal part and a flat layer of conidiophores. By gradual development the acervulus increases in size laterally, and usually also deepens, taking on a more spherical form. The basal part becomes compact, and its cell walls thick and brown. A covering of similar cells is absent or weakly developed except in winter acervuli (or pycnidia) in which it is typical. Adjacent fructifications may coalesce. From the conidiophores conidia are successively abjointed apically and to some extent from lateral branches. Conidial production continues during the entire vegetative season and even into the winter.

Whether this conidial stage should be referred to the genus Gloeosporium in accordance with Bubák and Kabát (1906), or to the genus Cylindrosporium in accordance with Gilman and Archer (1929), or to some other genus,<sup>8</sup> is a queston which lies outside the province of this paper. But as to identity, the conidial material from Massachusetts used in the experiments described in this paper clearly conforms to the description of Gloeosporium Pteridis (Rebent.) Bubák and Kabát in the form, size, and aseptate character of the conidia (Bubák and Kabát, 1906), while the fructifica-

<sup>&</sup>lt;sup>7</sup> For the synonymy of the imperfect stage, see also Bubák (1916), and Seymour (1929).

 $<sup>^8</sup>$  Von Höhnel (1925) makes the imperfect stage of this fungus the type of a new genus of the Fungi Imperfecti, *Cryptomycella Pteridis* (Kalchbr.) v. Höhn., emphasizing that "... der Pilz ein gut entwickeltes braunes Stroma besitzt und neben halb offenen auch geschlossene Fruchtkörper hat..." He also records the presence of a second type of conidium characterized by pointed ends and small dimensions  $(6-8 \, \mu \times 1.5 \, \mu)$ .

tions from which they arise are just like those described and figured by Killian (1918). That this American form is the same as the European one was further confirmed by the similarity in form, size, and manner of germination of conidia of *Cryptomycina Pteridis* collected in Massachusetts on the eastern bracken and of conidia of *Cryptomycina Pteridis* collected on the bracken of Europe near Stavanger, Norway.

#### THE DISEASE. REVIEW OF PREVIOUS INVESTIGATIONS

The disease and its causal fungus have been studied in detail by Killian (1918) only. His full and well illustrated account is based on field observations made from May to November, correlated with studies of fixed, sectioned and stained material of host and parasite, beginning with the young diseased fronds and carried through to the formation of ascospores on dead fronds the following spring. Although Killian has presented a complete picture of the life history of the parasite (to which frequent reference has been made in discussing the fruit bodies of the fungus), the present paper will consider in detail only those portions of Killian's investigations which deal with the relation of host and parasite—inoculation, incubation, infection, and appearance and distribution of the fungus hyphae in the tissues of the fern frond—, since these alone have a bearing on the studies presented in the present paper. lowing, then, is a synopsis of Killian's account as it bears on the relation between Cryptomycina Pteridis and its host:

Inoculation with ascospores occurs after rain, beginning about the middle of May and extending into June. Inoculation with conidia takes place from June into November. The ejected ascospores fall upon the surface of the wet fronds and, as the water drops evaporate, are drawn with the last traces of water by capillarity through the stomata of the lower epidermis into the substomatal chambers where they germinate.

(These conclusions in regard to inoculation were based on the study of sections of young, naturally infected fronds, in which structures interpreted as germinating spores were observed and figured by Killian. His attempts to germinate ascospores in drops of water on living pinnules of bracken in

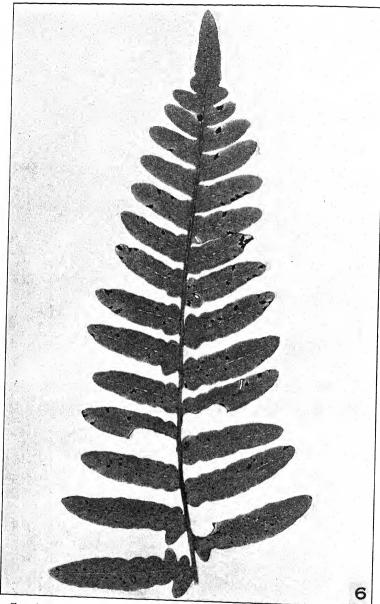


Fig. 6, pinna of diseased bracken from Ringwood, N. Y., × 1½, showing scattered localized lesions, many and small on older parts, few and large on younger parts—lesions similar in character and distribution to those on artificially inoculated fronds. (Photograph by Mr. W. R. Fisher.)

gave extremely variable results, while attempts to germinate ascopsores in drops of water on living pinnules of bracken in moist chambers failed completely, as did also all attempts to germinate conidia. Germination of ascospores and growth of an ascomycete were obtained on a solid medium from spores ejected from bits of dead, overwintered, infested fronds—but the fungus which developed was not *C. Pteridis*. It proved to be a saprophyte. Successful infection experiments in the natural habitat are mentioned but not described.)

Only young fronds which have just unrolled are attacked. Older fronds are immune, their immunity extending to the still embryonic tip.

In the beginning the hyphae are always intercellular. They grow in particular abundance in the substomatal chambers and adjacent intercellular spaces.

The incubation period varies in length. It is usually two days but may be six. (The maximum length of the period is not given. Killian regards the incubation period as the period elapsing between a spring or early summer rain sufficient to bring about soaking of dead infested fronds and subsequent ejection of ascospores, and the appearance of the first symptoms of disease in young fronds exposed to a shower of these spores.)

The first symptom of infection is the boat-shaped arching of the pinnules, making the lower surface concave. Later the foliage takes on a yellowish-green color, especially on the lower surface, contrasting with the blue-green color of healthy fronds. The yellowing involves the tissue between the veins, the veins themselves remaining normal in color. Symptoms characteristic of the further progress of the disease are the strong inrolling of pinnule tips and the upward lift of the pinnules. Brown dots, signalling the formation of conidial fructifications, appear in the yellow areas, followed by black dots which mark the initiation of ascus fructifications. The black spots grow and become confluent, finally occupying the intercostal areas as black stromata.

It is typical of most diseased fronds that the series of symptoms and signs described above appears first on the basal pin-

nae and progressively on the upper pinnae as these develop, until the whole frond is involved. Some fronds, however, show a lighter infection, with general symptoms of a less conspicuous nature. "Es ist nun bemerkenswert, dass hier die ältesten schwarzen Fruchkörper nicht wie sonst, regelmässig auf die ältesten Blattfiedern verteilt sind, sondern unregelmässig zerstreut vorkommen."

The explanation given of this difference in type of symptoms is a difference in resistance of the fronds. In a susceptible frond the fungus is assumed to spread rapidly through the tissues, primary infection becoming unidentifiable through the secondary vegetative spread of the fungus or by additional infections due to conidia. (Rapidly growing fronds may present a partial infection of this type in which the edges of the pinnules remain entirely unaffected.) In a resistant frond, on the other hand, it is assumed that the fungus meets with such opposition that its growth is limited ". . . mehr auf seine Ursprungsstellen, da eben, wo zufällig die Ascusspore hingeschleudert wurde," and the places of primary infection ". . . sind naturgemäss nach den Gesetzen des Zufalls zerstreut."

The development of typical symptoms is correlated with the activities of the fungus in the tissues of the host. Spreading out, according to Killian's interpretation, from the substomatal chambers, at first intercellular and forming a loose weft, the fungus later sends compact side branches into the host cells, attacking the nucleus and the chloroplasts, and finally reducing the cell contents to a formless lump. The hyphae within the cells show stronger growth than the intercellular mycelium and become much branched, filling the invaded cell. This invasion takes place near the infection courts, while farther away the hyphae are always intercellular.

In the substomatal chambers and adjacent regions, where the fungus grows most freely, are initiated the conidial fructifications.

The veins are not invaded by the fungus.

The hyphae are characterized by very thin walls, thickly granular cytoplasm, many vacuoles, and nuclei with variable

affinity for stains, in some cases staining intensely, in other cases faintly.

#### INVESTIGATIONS

PART I. STUDIES ON THE SYSTEMIC NATURE OF THE DISEASE

In the course of field observations beginning in 1926, the present investigator has been struck by certain aspects of the disease which indicate systemic infection.<sup>9</sup> The assumption that typically diseased fronds were infected with the mycelium of the parasite from the time of their initiation as buds was based on the following observations:

- 1. The characteristic abundance and even distribution of the stromata.
- 2. The appearance of symptoms first on the oldest (basal) pinnae and then progressively on younger pinnae.
- 3. The fact that when the lowest pinnae of a frond were healthy, the tip of the frond was also healthy, in spite of the well-known fern character of possessing a still embryonic tip while the lower pinnae are maturing. (These three observations were also made by Killian. He explained the first and second phenomena as due to the rapid spread of the invading fungus from the points of infection. He explained the third by assuming the development in the maturing portion of a frond of a resistance that extends to the younger parts.)
- 4. The slow spread of the disease. It was seen year after year in the same patches of bracken while neighboring ones remained healthy.

These were indications only. Evidence was sought along two lines of investigation: (1) Buds of rhizomes that had produced typically diseased fronds were examined microscopically in order to determine whether mycelium was present in their tissues; and

<sup>9</sup> Although the theory that in the leaf roll disease of bracken systemic infection is present has been expressed to the writer independently by more than one mycologist during the progress of these investigations, only two published statements that reflect such a view were found, namely those of Rostrup (1885) and Lind (1913), the second being based upon the first.

(2) rhizomes which had borne typically diseased fronds were transplanted into an environment where spore inoculation would be excluded, in order to determine whether new fronds produced under such conditions would also be diseased.

## A. Systemic Infection of Bracken Buds

Buds from bracken rhizomes bearing diseased fronds, and buds from rhizomes bearing healthy fronds were cut in pieces and fixed. Material from both sets of rhizomes was gathered in Ashfield, Mass., in late fall, and at Ringwood, near Ithaca, N. Y., in midsummer. Macroscopically, the buds from the two sets of rhizomes looked alike. Some of the buds were cut free-hand, others were imbedded in paraffin (52–54°) and cut into sections 5 to 17  $\mu$  thick. The stains chiefly used were thionin and orange G according to the method of Stoughton (1930), and Heidenhain's haematoxylin with light green. A fungus was found in all buds from rhizomes bearing diseased fronds, whereas no fungus was found in any of the buds from rhizomes bearing healthy fronds.

In order to determine the distribution and characteristics of the mycelium in the invaded buds, an intensive study was made of sections of one stem bud and one frond bud. For purposes of comparison, sections showing the mycelium of *Cryptomycina Pteridis* in typically diseased uncurled fronds of bracken were studied. In sections of both kinds of buds the distribution of the fungus in the tissues of the bracken was very patchy, neither evenly distributed nor concentrated in any particular tissue.

In the stem bud, the fungus was found in the following tissues: (1) Undifferentiated tissue of the tip, only 11 cells removed from the apical cell, (2) sclerenchyma (both that of the subepidermal sheath and that of the central strands), (3) cortical parenchyma, (4) endodermis, (5) pericycle, (6) phloem, (7) xylem. In the frond bud also, the fungus was present in cortical and in vascular tissues, and was seen also in the epidermis.

The fungus is both inter- and intracellular (FIGS. 9, 12–15). Near the tip of the stem bud, the cells of invaded areas are usually alive and normal in appearance even when the fungus is in contact with the nucleus, 10 which is often the case (FIGS. 10, 11). The

<sup>&</sup>lt;sup>10</sup> Later study of rapidly growing buds showed that the nucleus of an invaded cell may undergo mitosis (FIG. 16).

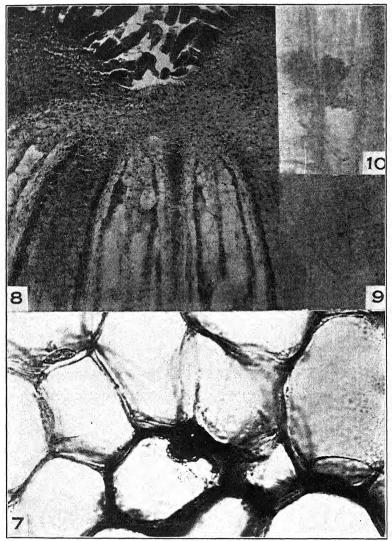


Fig. 7, cortex of systemically diseased bracken bud, × 500, showing dead cell with thickened, discolored walls and cluster of dead fungus hyphae; 8, portion of tip of bracken stem bud (diseased), × 92, long. section, showing large cells adjacent to apical cell (apical cell not included in section), undifferentiated tissue behind apical region, and differentiated tissues farther back; 9, intracellular mycelium in pericycle of diseased stem bud, × 631, long. section; 10, hyphae in contact with nucleus of pericycle cell, × 732, long. section. (Fig. 7 from photograph by Mr. W. R. Fisher; 8–10 from photographs made with the help of Professor Helen A. Choate.)

fungus hyphae are stout, and the intracellular mycelium is characterized by its prolific branching and its tendency to fill the entire cell (FIG. 13), as noted by Killian (1918) for intracellular mycelium of *Cryptomycina Pteridis* in frond chlorenchyma. It is easier to see the fungus in the tip of the bud than in portions a few millimeters behind the tip, since in the older parts the mycelium together with the walls of the invaded cells tends to take on a dark color. The invaded regions, however, are easily picked out because of this discoloration. These regions remain limited in extent, and in them the cells of both host and parasite appear to be dead (FIG. 7).

The tip of the frond bud with its invading fungus presents a picture similar to that presented by the tip of the infected stem bud.

When stained with thionin and orange G, the mycelium in the bud tips took on a bright yellow color, limited to the peripheral region of the hyphae, which made it easy to pick out areas of fungus invasion under the low power of the microscope. The cytoplasm of the hyphae stained faint bluish purple, the nuclei bright purple. Behind the stem tip, the bright yellow coloring was replaced by dirty yellow, and still farther back, as already described, the fungus tends to become dark. A brownish color was also characteristic of hyphae of C. Pteridis found in the vascular tissue of the uncurled frond. Some millimeters behind the frond tip, the yellow stain became lighter, while the cytoplasm took on a strong purplish color. The hyphae of C. Pteridis in the intercellular spaces of chlorenchyma in the uncurled frond varied greatly in diameter, thick and distinctly club-shaped branches being discernible here and there. The mycelium of these intercellular spaces had the thin walls and brightly-staining cytoplasm described by Killian (1918).

# B. Production of Diseased Fronds by Transplanted Rhizomes which had Previously Borne Diseased Fronds

In September, 1931, pieces of bracken rhizomes which had borne diseased fronds and pieces of rhizomes which had borne healthy fronds in Arnot Forest, Schuyler County, N. Y., were washed and transplanted to flats, wintered out-of-doors in Ithaca, N. Y., remote from any source of natural inoculation, and brought into the greenhouse in April and May. In the greenhouse, fronds appeared at irregular intervals from the beginning of May.

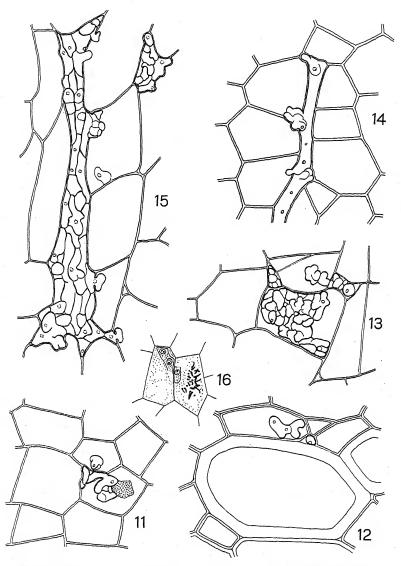


Fig. 11, inter- and intracellular mycelium of *Cryptomycina Pteridis* in young cortical tissue, long. section; 12, mycelium in xylem, cross section; 13, 14, mycelium in young cortical tissue, long. sections; 15, intercellular mycelium and haustorial branches in young phloem, long. section; 16, intracellular hyphae in undifferentiated tissue near apical cell, one of invaded cells in early anaphase, long. section. All figures about × 700. Thickness of walls of host cells somewhat exaggerated in figures 11, 13, 14, and 15.

All the fronds from rhizomes which had borne healthy fronds were healthy.

Of the fronds from rhizomes which had borne diseased fronds, some were healthy, but others showed typical symptoms of the disease when their pinnae unrolled, and later their lower surfaces became covered with the characteristic black stromata.

A second experiment of the same sort was run at Smith College, Northampton, Mass., with rhizomes dug in Ashfield, Mass., on October 16 and November 21, 1935. The flats were examined from time to time, and notes taken on the fronds which appeared. By July, 1936, observations were complete for 51 fronds from rhizomes which had borne diseased fronds, and by August 18, 1936, for 31 fronds from rhizomes which had borne healthy fronds.

All the 31 fronds from rhizomes which had borne healthy fronds were healthy.

Of the 51 fronds from rhizomes which had borne diseased fronds, 39 were diseased, 6 were healthy, and 6 showed doubtful traces of disease.

Observations made in 1937, 1938, and 1939 gave the same results: Healthy rhizomes continued to produce healthy fronds only. Diseased rhizomes continued to produce diseased fronds, but not all fronds produced by diseased rhizomes were necessarily diseased. And in at least one case, all fronds produced by such a rhizome appeared to be healthy.

In the case of a number of fronds from rhizomes which had borne diseased fronds, a young (rolled) portion of the frond was cut off before any macroscopic symptoms or signs of diseases were discernible, fixed, sectioned and stained in order that the presence or absence of the fungus at this early stage of development could be checked against the presence or absence of disease symptoms observed later in the maturing fronds. The immature fronds varied in height from 1.5 to 14 cm. The wounds were seared. The work was carried on from November, 1935, to June, 1936.

The observations made are recorded in table 1.

These data show that no fungus was found in pieces cut from young fronds which later showed no symptoms of disease, that the fungus was found in pieces cut from fronds which later showed

typical symptoms of disease, and that no fungus was found in the piece cut from the frond which later showed a few scattered lesions.

TABLE 1

MICROSCOPIC EXAMINATION OF PIECES CUT FROM YOUNG FRONDS
CHECKED AGAINST CONDITION OF SAME FRONDS WHEN MATURE

Date of cutting	Result of microscopic examination of pieces cut from young fronds: presence of fungus indicated by + absence of fungus indicated by -	Date of observation	Condition of mature frond: diseased condition = + healthy condition = -
Nov. 21 Nov. 21 Feb. 19 April 1 April 1 May 3 May 10 May 10 May 10 June 3 June 3	+ + + + + + + -	Feb. 12 Feb. 21 March 10 May 3 May 3 June 2 June 2 June 2 June 23 June 23 June 23 June 23	+ + + + + + + + + + + + + +

In order to determine the condition of a rhizome which had previously borne diseased fronds but from which healthy fronds now grew, a stem bud and a frond bud originating near the base of one of these healthy fronds were examined. No fungus was found in either bud.

On the basis of the evidence presented in Part I of this paper it is concluded that the leaf-roll disease of bracken is characterized by systemic infection. *Cryptomycina Pteridis* overwinters in rhizome buds and frond buds where it is present as inter- and intracellular mycelium in scattered areas of limited extent in the various host tissues, including the undifferentiated tissue of the extreme tip. During the growing season, its growth keeps pace with the growth of the stem buds, but the fungus does not spread in the maturing rhizome, remaining confined to limited areas where its cells apparently soon die. In the developing frond, however, its growth is luxuriant, especially in the intercellular spaces.

Killian (1918) considers infection by growth of the fungus mycelium within the host tissues in two connections:

1. To explain the very even and complete infection of typically diseased fronds.

2. As a possible cause of the infection of new sprouts from diseased fronds.

It is only one step further to consider the entire infection of such completely infected fronds as due to the growth of mycelium which has overwintered in the bud. This explains the completeness of the infection, the appearance of symptoms progressively on the maturing portions of the frond, and the apparent resistance of the tip when the base of the frond is not affected. It explains also the variability of the "incubation period" observed by Killian (1918) and the frequent shortness of this period (2 days), since the lapses of time thus recorded would be without significance if the bracken fronds were diseased before they appeared above ground.

This view involves a new conception of the development of the fungus in the tissues of the maturing frond. In the systemically infected frond the mycelium does not have its initial development as intercellular mycelium in the sub-stomatal chambers, spreading thence throughout the chlorenchyma (Killian, 1918). On the contrary, it is present as both intercellular and intracellular mycelium in scattered regions throughout the young frond, and spreads from some of these foci, reaching its greatest development in intercellular spaces and sub-stomatal chambers.

Of the fronds grown in the greenhouse from diseased rhizomes many show symptoms of what may be called incomplete systemic infection. The tips of the pinnae show no dark spots, or the upper portion of the frond shows none, or one side of the frond has many lesions and the other side few, or, as was seen in a single case, the lower pinnae show no lesions while the upper pinnae are typically diseased. It is easy to understand these partial infections when the patchy distribution of the fungus in the bud is recalled, for it then becomes clear how effectively the exclusion of the parasite from certain frond parts would follow the localized disturbance, in favor of the host, of the delicate balance between growth of the host and growth of the parasite.

Other fronds show symptoms of what may be called light systemic infection, characterized by the absence or weak development of the typical leaf-roll symptoms, and by few lesions. This type

of infection may be accounted for by a more profound disturbance of the growth balance in the parasite's disfavor.

#### PART II. GERMINATION AND INOCULATION STUDIES WITH CONIDIA

Among the questions left unanswered by the studies recorded in Part I were these:

- 1. Are the conidia and ascospores of *Cryptomycina Pteridis* capable of producing infection?
- 2. If so, are the symptoms of fronds that become diseased as a result of inoculation with conidia and ascospores similar to the symptoms presented by fronds developed from diseased buds?
- 3. At what stage of development of the bracken plant is systemic infection initiated?

Any attempt to answer these questions had to be based on inoculation experiments. These were confined almost entirely to experiments with conidia, for two reasons:

- 1. Ascospores may be obtained only in late spring and early summer from dead infested fronds wintered out-of-doors, while freshly produced conidia may be obtained through summer and fall from living diseased fronds in the field, and for several months longer from fronds grown in the greenhouse. Moreover, conidia on bracken fronds dried in the laboratory may retain their viability for over five months.
- Pycnidia as well as pseudothecia of Cryptomycina Pteridis are frequently found on dead, overwintered bracken fronds, and therefore washings from such fronds do not give an unmixed ascospore inoculum, conidia being present.

## A. Germination of Conidia

It will be recalled that Killian (1918) failed to obtain germination of conidia. In the present experiment their germination was observed on slides kept in moist chambers, in drops of the following sterilized and unsterilized liquids: distilled water, rain water, tap water, filtrate of humus in rain water. Germination was also observed in filtrates of water in which the following plant parts

had been bruised: fronds of the host (bracken), fronds of *Pteris longifolia* and of *Lygodium japonicum*, and leaf and bud of *Fittonia argyroneum*.

It must be emphasized, however, that the germination of conidia was extremely variable, which probably accounts for the negative results obtained by Killian (1918). But their germination in drops of filtrate of water in which bracken fronds had been bruised, although ranging from very poor to excellent, did not once fail completely, as did germination of conidia in water alone. It therefore seems probable that the presence of substances from the bruised frond of the host stimulates the germination of the conidia of the parasite.

Drops of the suspension of conidia used as inoculum in the experiments described in the next section were usually tested for germination. This varied from none to excellent, but it was found that germination on the slide was no criterion of germination on the host as indicated by infection, for a suspension in which not a single germinating conidium was seen on the slide proved just as effective inoculum as a suspension which showed excellent germination.

In germination, a germ tube is produced from either the end or the side of the conidium (FIGS. 5, 17–20). The production of two germ tubes by a conidium was rarely observed. The germ tube usually remains of limited length and unbranched, but sometimes a branch forms at its base.

## B. Inoculation Experiments

## 1. Inoculation of Fronds of Mature Plants

These experiments were carried out on young bracken fronds grown in flats in the Smith College Plant House from healthy rhizomes dug in Ashfield, Mass. Conidia for the inoculum came from diseased fronds grown in the same greenhouses. By means of an atomizer, the fronds were first sprayed with water and then with a heavy suspension of conidia in water. A moist atmosphere was insured by covering the sprayed fronds, together with an adjacent open container of water, with an inverted battery jar for 48 hours.

TABLE 2
INOCULATION OF YOUNG FRONDS WITH CONIDIA

	Inoculum		Inoculated fronds		Control fronds	
Date	Age	Medium of suspension	Num- ber used	Number becoming infected	Num- ber used	Number becoming infected
Feb. 21, 1937 March 12, 1937	Fresh 125 days 140 days 159 days Fresh Fresh	Sterile dist. water Tap water Sterile dist. water Sterile tap water Sterile dist. water Sterile dist. water	3 1 2 3 7 3	3 1 1 2 7 None	None None 1 2 3 2	None 1? None None

As will be seen from table 2, inoculation was followed by infection in all experiments except that of June 19, 1937. In this experiment the battery jars were temporarily removed after only 22 hours, and the results of the experiment were not checked until nearly three months from the time of inoculation, because of the unavoidable absence of the experimenter. In the two cases in which one of the fronds inoculated is recorded as not becoming infected (experiments of Feb. 21 and March 12), the frond was in the crosier stage.

While in the two preliminary experiments no controls were used, in the four subsequent experiments they were. The only possible case of infection of a control (experiment of March 12) is that of a single small brown spot on one of the lower pinnae of a frond which may have been in contact with an inoculated frond. When such contact was excluded, no controls showed any symptoms of disease.

The symptoms and signs of the disease on artificially inoculated fronds were: (1) dark leaf spots of various sizes, (2) dark, swollen, distorted areas involving varying amounts of blade, rachis, and stipe tissue, both types of lesions showing lighter areas around the dark regions, and (3) agglutinated masses of conidia on the surface of the spots and distorted areas.

In order to make a careful study of the character and distribution of infection areas on fronds artificially inoculated, the inoculation experiment of April 10, the general results of which are recorded in table 2, was carried out on seven fronds in different stages of development. A record was made of the height and the extent of expansion of each frond at the time of inoculation, and the distribution and nature of the infection areas that had appeared on each frond were recorded three weeks later.

TABLE 3

CORRELATION OF STAGE OF DEVELOPMENT OF ARTIFICIALLY INOCULATED FRONDS WITH NATURE AND DISTRIBUTION OF INFECTION AREAS

DEVELOPED AS A RESULT OF INOCULATION

Stage of developme of inoculation,	nt of fronds at time April 10, 1937	Nature and distribution of infection areas developed as recorded on May 1, 1937		
Height of frond in centimeters	Number of pairs of expanded pinnae	Pairs of pinnae showing infection	Pairs of pinnae having largest number of lesions	
1.5 12. 13. 10. 13. 22.	0 0 1 3 6 6 8	1st an d2d* 1st and 2d 1st-4th 3d -8th 5th-10th 5th-8th 6th-8th	1st and 2d 4th–6th 6th and 7th 6th and 7th	

<sup>\*</sup> And rachis opposite 5th pr. of pinnae.

These records are summarized in table 3. It was also noted that when lesions characterized by large size and by distortion were present, they were limited to pinnae unexpanded at the time of inoculation.

From this experiment are drawn the following conclusions:

- (1) Only young fronds and young portions of older fronds of bracken are susceptible to infection by conidia.
- (2) The "resistance" of the mature portions of a frond does not impart resistance to the immature portions of the same frond, contrary to the supposition of Killian (1918).
- (3) The heaviest infection (as measured by the number of infected areas) is found on pinnae which have just expanded or are in the act of expanding at the time of inoculation.
- (4) The greatest susceptibility (as measured by the size and degree of distortion of the infected areas) is found in the unexpanded pinnae of a frond. But the number of lesions on these pinnae is small, obviously because they were pro-

tected by their inrolled position, and for the same reason the tip may be entirely free from lesions.

Artificially inoculated fronds never showed the inrolled edges and arched pinnules characteristic of young diseased fronds in the field, nor the equally typical later development of evenly distributed, intercostal stromata (FIG. 2). Since these symptoms and signs were lacking, and since Part I of this paper has shown them to be invariably associated with systemic infection of the host, it is concluded that such symptoms are characteristic only of diseased fronds which arise from systemically infected bracken plants.

On the other hand, the symptoms and signs characteristic of artificially inoculated fronds were somewhat similar to those described by Killian (1918) on certain lightly infected fronds observed in the field, of which he says: "Solche wenig befallenen Farnpflanzen dokumentieren sich auch dadurch, dass die Krankheitssymptome im allgemein wenig ausgeprägter Natur sind. Es ist nun bemerkenswert, dass hier die ältesten schwartzen Fruchtkörper nicht wie sonst, regelmässig auf die ältesten Blattfiedern verteilt sind, sondern unregelmässig zerstreut vorkommen." Such fronds, showing conidial fructifications, however, rather than "black fruit bodies," have been found also by the present investigator, and one of them, collected at Ringwood, near Ithaca, N. Y., is shown in figure 6. Although its lesions are irregularly scattered, it is noteworthy that the older portions of the frond have many, small lesions, while the younger parts have fewer, larger lesions. This diseased frond bears the closest possible resemblance to fronds artificially inoculated with conidia.

However, in the case of a *lightly* infected field frond showing absence of leaf-roll symptoms and a few leaf spots, it may be impossible to determine from symptoms alone whether the frond has become diseased as a result of inoculation with spores, or whether, as indicated in Part I of this paper, it may have arisen from a systemically diseased rhizome.

Although no inoculated fronds showed any symptoms of systemic infection, yet it seemed theoretically possible that mycelium of the fungus could grow downward through the stipe of a very young frond, reach a rhizome bud, and there initiate systemic infec-

tion. Therefore fronds which appeared subsequent to inoculation in flats used in inoculation experiments were examined, but no frond showing symptoms of systemic infection ever appeared. Nor did any of the fronds show signs of localized infection, except two which came up in the same flat only 3.3 and 4 cm. from inoculated fronds, not long after inoculation. One of these showed a single lesion and the other a number of scattered lesions on the tip of the frond. Their infection was doubtless due to conidia from one of two sources: the soil of the flat which, uncovered at the time of inoculation, had received a rain of conidial suspension, or the conidial masses which oozed from the lesions of the inoculated fronds close by.

#### 2. Inoculation of Soil and of Underground Parts

Inoculation of the soil in which healthy bracken plants were growing, and inoculation of underground parts of the bracken exposed by digging or washing, were also tried, using suspensions of freshly collected conidia in sterile distilled water as inoculum. None of these experiments resulted in the systemic infection of the bracken. Inoculation of underground parts exposed by digging or washing resulted in some localized infection of fronds, the lesions being of the large, distorted type characteristic of infection resulting from inoculation of unexpanded frond parts above ground.

## 3. Inoculation of Spores and Gametophytes

Experiments were undertaken to find out whether young bracken plants (sporophytes) become infected with *Cryptomycina Pteridis* through the presence of the fungus upon (or within?) the bracken spores or through inoculation of the gametophytes from which the young sporophytes later arise.

Spores from healthy bracken plants came from Ringwood, near Ithaca, N. Y. Spores from diseased bracken and conidia for inoculum came from diseased fronds in the Smith College Plant House.

When bracken spores were disinfected, the spores were shaken up with filtrate of 10 grams calcium hypochlorite in 125 cc. dis-

tilled water in a 10 mm. test tube, left for 10 to 15 minutes, and transferred by means of a flamed loop from filtrate directly to slant.

The bracken spores were sown on large test tube slants of synthetic medium. Development of gametophytes was followed by development of sporophytes. Whenever it appeared necessary, sterile distilled water was added to the cultures to prevent drying. The experiments were started in October, 1936.

Four slants were sown with undisinfected and three with disinfected bracken spores obtained from *diseased* bracken fronds.

Three slants previously sprayed with a suspension of conidia in sterilized water were sown with undisinfected spores from healthy fronds.

Four slants of young gametophytes (developed from disinfected spores from healthy fronds) were inoculated with a suspension of conidia in sterilized water.

The bracken sporophytes which subsequently developed in these tubes, like the sporophytes which developed in control tubes, showed no symptoms of being infected with Cryptomycina Pteridis. There is therefore no evidence that sporophytes become infected through the gametophyte generation, since no infected sporophytes developed in (1) gametophyte cultures grown from spores of discased bracken, (2) gametophyte cultures grown from inoculated spores, (3) cultures of inoculated gametophytes.

## 4. Inoculation of Young Sporophytes

## a. Inoculation of Sporophytes in Test Tubes

Eleven young sporophytes in test tubes (developed in cultures from disinfected spores of healthy bracken) were inoculated with conidia in March, 1936.

By June two plants showed conidial fructifications from which conidial cirrhi were forced out. The conidia were like those of Cryptomycina Pteridis, measuring  $10{\text -}15~\mu \times 4{\text -}5~\mu$ . No signs of similar infection appeared on sporophytes of control tubes. The cramped plants were transferred to pots of sterilized humus in July, but did not survive transplanting, and no evidence as to whether or not the infection was systemic was therefore obtained.

Test tube cultures were satisfactory for experiments with

bracken spores and gametophytes. They were unsatisfactory for the growing of bracken sporophytes because of the small number of plants per tube and the difficulty of transferring plants from agar to soil. Moreover, all cultures became contaminated. Contaminants were of course introduced with the inoculum in all the inoculation experiments since the conidia were obtained from the surface of fronds, but control tubes also became contaminated in the course of the months necessary for the experiments, months during which irrigation of the cultures was necessary.

Another method of growing young sporophytes was therefore followed.

## b. Inoculation of Sporophytes on Inverted Flower-Pot

Abundant growth of young sporophytes attached to gametophytes was obtained in November, 1937, from bracken spores sown in July on the outer surface of a flower-pot filled with sphagnum, inverted in a shallow dish of water, and covered by a bell glass with open tubulated top.

The sporophytes were small, with the axis still vertical and undivided, the axis with its leaves having a height of about one to two centimeters.

Three areas of pot surface, from edge to bottom, were then stripped of plants, thus leaving three areas of young sporophytes separated from each other by bare areas. The plants in two of the areas were inoculated with a suspension of conidia in sterile distilled water, while those of the third area were left as controls, being sprayed with water only.

Leaf spot lesions developed on the fronds of several plants of the inoculated areas, while none were found on plants of the control area. Conidia from an exuded mass were typical of those of Cryptomycina Pteridis in form and size, measuring  $11-16 \, \mu \times 4 \, \mu$ .

Stained sections of the sporophyte on which the mass of conidia was found showed a fungus parasite in the embryonic region of its stem and in the youngest leaf primordium, as well as in older parts of the plant. The intra- and intercellular mycelium was just like that of *Cryptomycina Pteridis* in buds of mature, systemically infected bracken plants. Only four uninvaded cells separated the

parasite from the apical cell. In several invaded cells the nucleus was undergoing mitosis.

The conclusions drawn from this experiment and those drawn from the next experiment will be summarized together at the end of Part II.

#### c. Inoculation of Sporophytes in Soil

Three young sporophytes transplanted from pot surface to soil in November were inoculated in April with a suspension of conidia in sterile distilled water, while a fourth plant, the control, was sprayed with water only. In all four plants a portion, at least, of the rhizome system bearing young crosiers was still exposed above the surface of the soil, and the inoculum was directed particularly at the young rhizomes and buds. Some of the inoculum fell on the fronds also, and typical localized frond lesions were later observed on two of the inoculated plants.

In the middle of July, one frond of an inoculated plant showed symptoms of systemic infection, exhibiting the arching of pinnules characteristic of fronds arising from infected rhizomes. A second, younger frond adjacent to the first soon showed the same symptoms, followed by a third. No such symptoms of disease appeared in the two other inoculated plants nor in the control plant.

Typical early symptoms were followed by formation of conidial fructifications, from which conidia oozed. These were typical *Cryptomycina Pteridis* conidia in form, manner of germination, and size, those measured being 9–14.5  $\mu \times 3.5$ –5.5  $\mu$ .

Healthy fronds of bracken inoculated with these conidia developed typical localized lesions with typical conidial fructifications and conidia.

Free-hand sections of rachises of pinnae of diseased fronds of the young sporophyte showed the fungus to be present between and within the bracken cells. Its appearance and distribution were the same as the appearance and distribution of *Cryptomycina Pteridis* mycelium in similar sections of a typically diseased frond developed from a diseased rhizome planted in the greenhouse.

When sectioned and stained, the stem bud of the rhizome was found to be infected with mycelium. In the undifferentiated tissue

of the tip only two cells separated the parasite from the apical cell. A sectioned frond bud also showed typical infection.

The results of this experiment and of the preceding show that (1) a systemic infection of bracken, characterized by the presence of a parasite in the undifferentiated tissues of stem buds and leaf primordia, and by the development of diseased fronds from diseased leaf buds, may be initiated in young sporophytes by inoculation with conidia of Cryptomycina Pteridis, and that (2) this disease is identical with the leaf-roll disease of bracken, and that the parasitic fungus which causes it is identical with Cryptomycina Pteridis, the cause of leaf-roll disease.

## PART III. STUDIES ON PENETRATION AND EARLY STAGES OF INFECTION

It will be recalled that the attempts of Killian (1918) to germinate ascospores on pinnules of bracken in moist chambers met with failure, as did also attempts to germinate conidia, and that his conclusions as to the way in which C. Pteridis gains entrance into its host were based on study of fronds "... die in die Natur unter ganz normalen Bedingungen der Infection durch den Parasiten ausgesetzt gewesen waren." He found attached, germinating spores on both surfaces of the frond, but no evidence of penetration, and he interpreted as ascospores germinating in sub-stomatal chambers structures which his accurate drawings indicate to be simply thickened branches of mycelium in diseased fronds which were undoubtedly developed from diseased buds of systemically infected bracken plants. Similarly, his excellent illustrations and in most points perfectly accurate descriptions of "early" stages of frond infection do not apply to early stages at all, but to intermediate stages in the development of a systemic mycelium. (This point has been more fully discussed in Part I.)

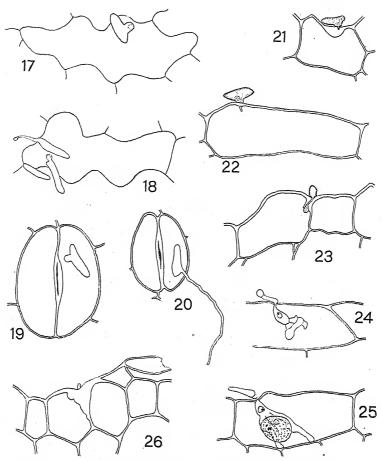
With the systemic nature of the disease demonstrated, it becomes clear that reliable data on penetration and early stages of infection can be gathered only from studies of artificially inoculated fronds from healthy rhizomes. Therefore, young fronds of healthy bracken in the greenhouse were sprayed with conidia of *C. Pteridis* in sterile distilled water. Small pieces of inoculated pinnules for sectioning were fixed in formalin-acetic-alcohol after 8 hours, 24

hours, 2, 3, and 4 days; while large pieces for surface examination were fixed after 2 days in a mixture of equal parts of acetic acid and 95 per cent alcohol. The large pieces were cleared in chloral hydrate, washed, and stained with cotton blue (12 minutes) or lactic blue (30 minutes). The better staining was obtained with cotton blue.

Examination of frond surfaces showed many germinating conidia on both surfaces of the frond. Their germ tubes varied in length. They were as likely to grow away from stomata as toward them (FIGS. 19, 20), and one tube was seen growing across a stoma. The germ tubes often followed the lines of radial walls of the epidermal cells. Frequently the germ tubes grew toward germ tubes of other conidia of the fungus. A small, brownish ring could usually be distinguished, outlining an area of the tube which was closely appressed to the surface of the host (FIGS. 17, 18). This area of the germ tube will be referred to as the appressorium.

Stained microtome sections showed that after 8 hours many conidia had germinated and formed appressoria. After 24 hours, penetration of the epidermal wall was taking place or had just been accomplished, by means of a minute peg-like outgrowth from the appressorium. Such a penetration tube, growing into a radial wall, is seen in figure 21. (The section shows only a portion of the obliquely cut wall.) In figure 22, the penetration tube has reached the lumen of the cell through the outer epidermal wall, which has become slightly thickened in the region pierced. Figure 23 shows a longer penetration tube which has grown within the radial walls of two adjacent epidermal cells and then sideways into one of these cells, where a vesicular swelling has formed at the tip of the penetration tube. Cells of both the upper and lower epidermis were penetrated by the fungus.

Sections of material fixed 2 days after inoculation in some cases showed large vesicular swellings of the mycelium of the parasite within the penetrated cell. In other cases, considerable branching of the mycelium within the host cell had taken place, as illustrated by figure 25, where several haustorial branches are in contact with the nucleus of the host cell. In still other cases the fungus had failed to complete penetration of the wall of the epidermal cell of



Figs. 17, 18, germinating conidia of *Cryptomycina Pteridis* on upper epidermis of young bracken frond, surface view; 19, 20, germinating conidia on guard cells of lower epidermis, surface view; 21, conidium with penetration tube in radial wall of epidermis, cross section, 24 hours after inoculation; 22, conidium with penetration tube which has pierced outer wall of epidermal cell, 24 hours after inoculation; 23, conidium with penetration tube and vesicular swelling, 24 hours after inoculation; 24, vesicular swelling with hyphal branches, 2 days after inoculation; 25, hyphae in contact with nucleus of host cell, 2 days after inoculation; 26, incomplete penetration, radial wall of epidermis thickened and discolored, 4 days after inoculation. All figures about × 700.

the host, and this failure was apparently correlated with abnormal changes in the cell wall, which had become thick and dark in color below the appressorium (FIG. 26). It also appears probable that when the fungus has grown through the epidermal wall it is sometimes unable to spread beyond the first cell invaded. This is indicated by certain sections of material fixed 4 days after inoculation which show a thick, dark sheath around the parasite, which is still confined to a single host cell.

When invasion is successful, however, the fungus grows rapidly from cell to cell, being found in material fixed 4 days after inoculation as far as the fifth row of cells from the surface of the invaded epidermis. Since the leaf was 8 cells in thickness in this region, the mycelium had advanced more than half way through the leaf.

In the preparation of material for the above study of germination and early stages of infection, only conidia were used as inoculum. For reasons already stated, ascospores are obtainable only in late spring and early summer and it is difficult to obtain ascospore inoculum uncontaminated with conidia. However, experiments with ascospores are in progress and will be reported on in a later paper.

#### SUMMARY

Cryptomycina Pteridis (Rebentisch ex Fries) von Höhnel, cause of leaf-roll of bracken, was studied in its relationship to Pteridium latiusculum (Desv.) Hieron ex R. E. Fries, the eastern bracken.

- 1. The fungus is systemic and perennial, overwintering in stem buds and frond buds of its host, and persisting indefinitely in a given diseased plant.
- 2. The mycelium of the parasite was not found in the apical cell of the stem bud, but in the undifferentiated tissue adjacent to it, separated from it by from 2 to 11 uninvaded cells. The mycelium is both inter- and intracellular. It was occasionally seen in a bracken cell the nucleus of which was undergoing mitosis.
- 3. In the maturing rhizome, which gives no external evidence of being diseased, the scattered infection areas in the various tissues remain of limited extent, and the fungus apparently dies. In the maturing frond, which exhibits striking symptoms of being

diseased, the fungus spreads from originally scattered foci and develops with marked luxuriance.

- 4. Typical symptoms and signs of leaf-roll disease are found only in fronds developed from diseased buds of systemically infected plants.
- 5. Inoculation, with conidia, of young fronds or of immature portions of older fronds was followed by infection resulting in localized lesions.
- 6. Inoculation, with conidia, of young bracken sporophytes was followed by infection resulting in systemic infection and typical leaf-roll symptoms.
- 7. No systemic infection of mature plants followed the inoculation, with conidia, of (1) their fronds, or (2) the soil covering their underground parts, or (3) the underground parts themselves.
- 8. No systemic infection of young sporophytes followed the inoculation, with conidia, of bracken spores or young gametophytes.
- 9. Germination of conidia was obtained in various liquids and on the surface of young bracken fronds.
- 10. The fungus enters the host by sending a penetration tube through the wall of an epidermal cell. The hyphae grow rapidly from cell to cell.

Specimens of material used in the above experiments and observations have been deposited in the Herbarium of the Department of Plant Pathology of Cornell University, the Farlow Herbarium of Harvard University and the Herbarium of the Bureau of Plant Industry.

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# MYCOLOGICAL NOTES FOR 1936-38 1

L. O. OVERHOLTS

(WITH 14 FIGURES)

This paper is a continuation of a series with similar title begun in 1919 and continued until the present time. They represent an attempt to throw light on the new and unusual fungi encountered from year to year, especially those inadequately known or lacking complete descriptions and illustrations.

#### ASCOMYCETES

APOSTEMIDIUM VIBRISSEOIDES (PECK) BOUD. (FIG. 3)

Although I had searched for this fungus for years in central Pennsylvania, it was not collected until the summer of 1938, and then only in limited amounts. Since Durand lists it only from New Hampshire, Vermont, and New York, it is likely that Pennsylvania is on the southern limits of its range. I have seen no published photo of an American collection.

### CENANGIUM GRISEUM DEARN. & HOUSE (FIG. 8)

Collected at Laurel Run, Huntingdon County, Pa., June 30, 1938, on dead *Acer rubrum*. The original host was *A. spicatum*. I collected this fungus in Ontario with Dr. H. S. Jackson. On securing the Pennsylvania material I suspected the identity of the fungus and sent part of it to Dr. Dearness, who verified the determination. The species was originally described from Ontario. In my Pennsylvania material the disk of the apothecium is much more olivaceous tinged than in the Ontario material.

<sup>&</sup>lt;sup>1</sup> Authorized for publication on May 16, 1939, as paper no. 906 in the Journal Series of the Pennsylvania Agricultural Experiment Station. Contribution no. 126, Department of Botany, The Pennsylvania State College, State College, Pa.

# CORYNETES ROBUSTA DURAND (FIG. 1)

When Durand wrote his monograph on Geoglossaceae in 1908 he reported this species from only Maine, Massachusetts, New York, North Carolina and Mississippi. In the summer of 1937 it was abundant in one locality along Stone Creek, Huntingdon County, Pa. Appearing about August 18, the specimens developed slowly until about September 10. Although the spot is one visited

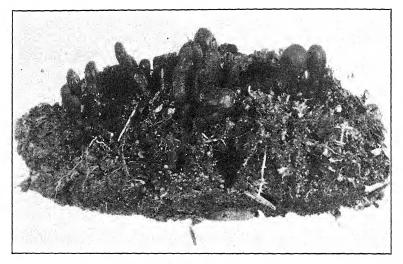


Fig. 1. Corynetes robusta.  $\times$  1.

several times in late summer and fall collecting every year, the fungus had never previously been seen there and it did not reappear in the season of 1938. Further evidence of the rarity of the species of *Corynetes* is the apparent fact that Peck never collected or at least never reported anything under that generic name. The photo presented herewith is of plants at the time the colony was first discovered—hence quite immature. I have a photo that would duplicate Durand's illustration.

# MYCOSPHAERELLA SARRACENIAE (SCHW.) HOUSE

Perithecia crowded over the stem surface, appearing as small black emergences without definite arrangement, 50–70  $\mu$  diameter; asci pyriform to ellipsoid or subglobose,  $18-24 \times 12-14 \mu$ , 8-

spored; spores oblong or somewhat narrowed at one end, smooth, hyaline, 2-celled, 12–16  $\times$  3.5–4  $\mu$ .

On dead flowering stalks of *Sarracenia purpurea*. Lopez, Sullivan County, Pa., September 11, 1936. The species was originally described from the Carolinas. House (1921) reported it from New York, on both leaves and peduncles. I know of no other reports of its occurrence. I find the spores to be somewhat larger than in the original description.

#### TAPHRINA FILICINA ROSTR.

Recent advances in our knowledge of the species of this genus have been considerable. The above species is listed by Mix as known only from the vicinity of Ithaca, New York. A collection made in McKean County, Pa., on *Aspidium spinulosum* in 1938 was sent to Mix and he pronounced it as correctly determined. The fungus was abundant over a considerable area in the McKean Forest, near Mt. Jewett, Pa.

#### FUNGI IMPERFECTI

# Cercospora Polemonii sp nov.

Spots indefinite, bounded by the larger veins, occupying a large part of the leaf surface; conidia hypophyllous, appearing under a lens as a fine smoky scurf, the conidiophores fasciculate, short,  $20\text{--}30 \times 5\text{--}5~\mu$ , brownish; spores elongate, subhyaline to somewhat smoky, 1-celled then up to 4-celled, straight, clavate-cylindric,  $32\text{--}60 \times 2.5\text{--}5~\mu$ .

The type of this species was collected on living leaves of *Polemonium reptans*, State College, Pa., September 19, 1912, by J. B. Demaree. Overholts Herbarium 11690.

This is the collection reported in Mycologia 30: 269. 1938 as *C. omphakodes*. Dr. Charles Chupp informs me that reference could hardly be correct.

# CORNULARIA PERSICAE (SCHW.) SACC.

Pycnidia erect, spiniform, flexible when wet, rigid and brittle when dry, black, 800–1000  $\mu$  high, about 125  $\mu$  diameter, under the microscope the walls roughened by the protruding ends of narrow, brown or blackish hyphal tips; conidia elongated, straight or slightly

curved, 7–10-celled, brownish except for the hyaline terminal cells, 64–80  $\times$  3.5–4  $\mu$ .

On dead branches of *Prunus* sp. (probably a plum). State College. Pa., December 15, 1937. A most inconspicuous fungus that I am not able to enlarge enough to present a photo. Apparently rare.

#### EXOSPORIUM TILIAE LINK (FIG. 7)

Stromata 0.5–1 mm. diameter and about as high, erumpent, subglobose to depressed-globose and somewhat pezizaform, black, appearing powdery, waxy when wet, becoming hard on drying; in section composed of nearly colorless hyphae, with a definite black cuticular layer made up mainly of the blunt conidophores 10–12  $\mu$  diameter and about as high, dark-colored; conidia clavate, dark colored, 60–80  $\times$  16–17  $\mu$ , indistinctly transversely septated into a number of cells, the walls very thick.

On dead branches of *Tilia*. Collected at the foot of Mt. Davis, Somerset County, Pa., July 15, 1938. Though listed in the Seymour Index, I have seen no other reference to this fungus in America. Superficially and without magnification it resembles *Strumella*, but under a lens the stromata are more firm and decidedly cupuliform in many cases, simulating a *Cenangium*.

#### PHYLLOSTICTA GUTTULATA HALSTED

Seaver reports this species from only Vermont and New York. A collection was made at State College, Pa., September 19, 1931, on *Oxalis stricta*. The pycnidia are unusually large, measuring up to  $200 \mu$  diameter.

#### PHYLLOSTICTA MACROSPORA ELLIS & EV.

On living leaves of Liriodendron Tulipifera there is a common spot, perhaps of insect origin, that serves as a substratum for at least four different species of fungi in Pennsylvania. A species of Cladosporium forms a white floccose pubescence on the lower surfaces of some of the spots. A Phyllosticta which seems referable to P. liriodendrica is sometimes present with elliptic spores  $5-8\times3-5~\mu$ . Again there is sometimes present a spermogonial stage of Mycosphaerella Liriodendri (Cooke) which seems never

to have been transferred from the old genus *Sphaerella*, and of which *Phyllosticta liriodendrica* has been said to be the conidial stage. There is also at times another *Phyllosticta* with spores  $15-17 \ (-22) \times 4-6 \ \mu$ . This agrees with the spore measurements of *P. macrospora*. That species, however, Seaver (N. Am. Flora 6: 44. 1922) thinks, may have been based on an immature ascus stage of the *Mycosphaerella*. However, I have demonstrated

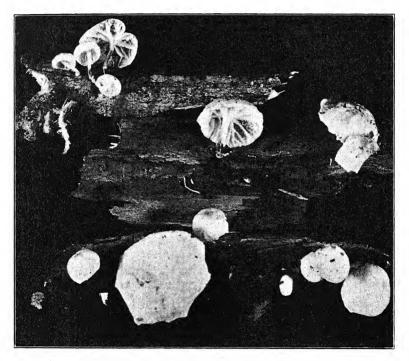


Fig. 2. Marasmius magnisporus.  $\times$  1.

clearly that there is on these spots a large spored *Phyllosticta* which would answer the description of *M. macrospora*. It is quite possible that the type collection of that species may have included two fungi and that in examining the collection Seaver may have obtained only the immature ascus stage of the *Mycosphaerella*. Collections were made in Center County, Pa., in 1938.

#### RAMULARIA OXALIDIS FARLOW

Spots circular, elliptic,  $3-5\times 2-4$  mm., single on the leaflets, the center grayish, with a rather broad, red-brown, conspicuous margin; conidiophores hypophyllous as a thin white pubescence, densely fasciculate,  $50-70\times 2-3~\mu$ , septate, hyaline; conidia clongate, 1-celled then mostly 2-celled, occasionally 3-celled,  $14-24\times 3-4~\mu$ .

On living leaves of Oxalis acctosella. Although a spot had been observed on leaves of this host for many years, no fruiting was collected until 1938 when it was found in quantity near Halsey, McKean County, Pa. I have seen some evidence that this fungus would be better referred to Septocylindrium, since in a few cases the spores were seen in chains of two. This point needs further investigation. The original description referred to the rarity of septated spores but I find the septa well developed and conspicuous. The species was originally reported from New Hampshire on this host. The only other record I have seen is that of Dr. Davis from Wisconsin on an unspecified species of Oxalis.

#### Septoria longispora sp. nov.

Spots narrow-elliptic or somewhat elongate, 5–7 mm. long, 1–2 mm. broad, not coalescing, somewhat more conspicuous from above, uniformly brown, scarcely becoming pallid, definite, and with a slightly darker margin; pycnidia minute, 60– $80~\mu$  diameter, black, poorly dfferentiated, epiphyllous, scattered; spores linear, smooth, hyaline, 40– $95~\times~1.5~\mu$ , apparently 4-celled but the septa indistinct.

On living leaves of *Aquilegia canadensis*. Type collected at State College, Pa., September 15, 1931. W. L. White. Overholts Herbarium 21450.

The spores are much too long for any species listed as occurring on this or related hosts.

#### SEPTORIA SPICULOSA ELLIS & HOLW.

The original description can be supplemented as follows: spots irregularly elongate, equally visible from both surfaces, 1–2 cm. long, 5–8 mm. broad, smoky brown, not sharply delmited; pycnidia epiphyllus; spores  $25–35 \times 1.5 \mu$ , and about the size and shape of the cell crystals of the host.

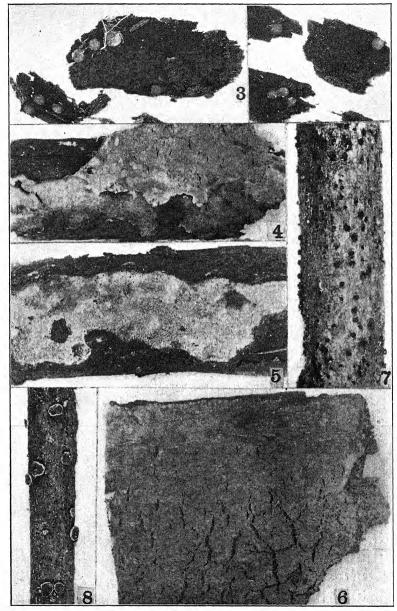


Fig. 3. Apostemidium vibrisscoides,  $\times$  1½; 4–6, Poria albobrunnea,  $\times$  1; 7, Exosporium Tiliae,  $\times$  1½; 8, Cenangium griseum,  $\times$  1½.

On yellow leaves of *Symplocarpus foetidus*. Charter Oak, Huntingdon County, Pa., July 13, 1930. The fungus is accompanied by a species of *Vermicularia*. Originally described from Wisconsin and Dr. Davis included it in his reports from that state. I have seen no other references to its occurrence, hence this collection extends its range considerably.

#### SPHAERONEMA MAGNOLIAE PECK

The original description can be supplemented as follows: pycnidia 1–2 mm. long; conidia hyaline, 9–10  $\times$  5–6  $\mu$ ; conidiophores hyaline, slender, 20–40  $\times$  2–3  $\mu$ , tapering to the apex.

On dead twigs of Magniolia acuminata, Laurel Run, Huntingdon County, Pa., March 13, 1936. The species was originally described from New York. I have seen no other references to its distribution.

#### THYRSIDIUM HEDERICOLA VAR. CARPINI SACC.

Fruiting structures in the form of mound-like, soft-gelatinous masses 1–2 mm. diameter, or confluent and larger; in section composed of hyaline, erect or suberect hyphae, simple, each bearing a rounded blackish head of spores, 30–40  $\mu$  diameter; spores held together in a gelatinous ball, globose, smooth, olivaceous, 3.5–4.5  $\mu$  diameter, borne in chains.

On dead branches of *Carpinus caroliniana*. Mt. Davis, Somerset County, Pa., July 15, 1938. The Seymour Index lists this species but otherwise I have seen no American records of it. It is a curious fungus. The catenulate arrangement of the spores within the heads is not apparent yet must be inferred when the very young heads are compared with mature ones.

#### BASIDIOMYCETES

### BOLETUS MIRABILIS MURRILL (FIGS. 13, 14)

Collected at Ross Run, Huntingdon County, Pa., September 6, 1937, on the ground under white pine trees. This species is known otherwise only from Manitoba and the Pacific Coast, writes Dr. Snell to whom specimens were sent for identification. The spores measure  $20\text{--}26 \times 8\text{--}9~\mu$ . The very dark red pileus that is strongly viscid (Van Dyke Red or Madder Brown, R.), the rugose or papil-

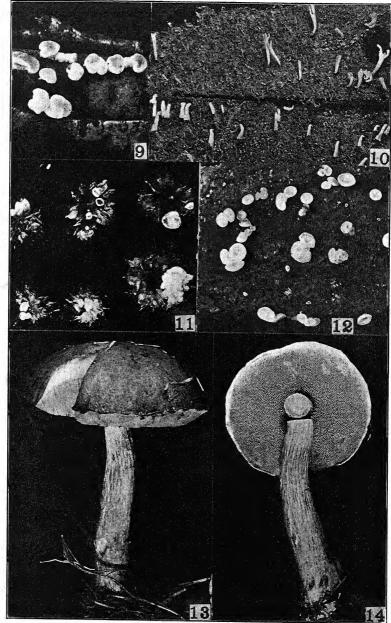


Fig. 9. Femsjonia luteoalba,  $\times$  1; 10, Craterellus cristatus,  $\times$  34; 11, Cyphella muscigena,  $\times$  1½; 12, Guepinia pennsylvanica,  $\times$  1½; 13, 14, Boletus mirabilis,  $\times$  34.

late pileus, the long narrow reticulations and the pinkish color of the stem are the diagnostic features. The stem reticulations are well developed and this with the pinkish color is strongly reminiscent of such species as *B. Betulae* of the Laceripedes group.

## CRATERELLUS CRISTATUS KAUFF. (FIG. 10)

Sporophore clavate or subcylindric, erect, 7–15 mm. high, simple or occasionally branched once or twice near the apex which is expanded and truncate or with 2 to 4 coronate tips, color purplish gray, soft and fleshy, glabrous, narrowed downward, gregarious; spores short-cylindric, smooth, hyaline,  $5-6\times2.5-3~\mu$ ; gloeocystidia numerous, appearing as the projecting tips of long flexuous conducting cells  $4-8~\mu$  diameter.

On mossy coniferous log. Camp Mercier, Laurentides National Park, Quebec, August 27, 1938. R. F. Cain.

Whether this properly belongs in *Clavaria* or in *Craterellus* is a question. The situation is akin to that of the proper disposition of *Clavaria pistillaris* which has been placed in both genera. My specimens are smaller than those described by Kauffman who found the sporophores up to 2.5 cm. high. Otherwise the agreement is excellent. Kauffman's specimens were collected in Oregon.

# CYPHELLA MUSCIGENA FRIES (FIG. 11)

Sporophore grayish-white to isabelline, campanulate to inversely conic, 1–5 mm. diameter, the pileus sessile and attached by the vertex, finally becoming expanded; hymenium concolorous, smooth, or in large plants slightly rugose, the entire sporophore thin, pliant; spores oblong-ellipsoid, smooth, hyaline,  $7-10 \times 3.5-5 \mu$ ; cystidia none; basidia  $18-20 \times 6-7 \mu$ , 4-spored.

On living mosses, e.g., Bryum roseum. A collection of this unique fungus was made at Slippery Rock, Butler County, Pa., in 1938. The sporophore seems to be attached underneath the crown of leaves of the Bryum plants, where it is pendent, apparently attached at or near the leaf bases. In the Pennsylvania plants there is no indication of a stem. Bourdot and Galzin say that Burt's plants under this name cannot represent the species, differing in structure and in smaller spores. Burt gives the spores as  $4.5-5 \times 2.5-3 \mu$  and says these measurements follow those of European

exsiccati and likewise of Bresadola. But Bourdot and Galzin say that Bresadola's description in Fungi Polonoci apply in part to Arrhenia auriscalpium. They give the spore measurements as  $7.5-9-12 \times 4.5\mu6 \mu$ , with which my plants agree well.

#### Guepinia pennsylvanica sp. nov. (FIG. 12)

Sporophores single or more frequently in clusters of 2 to 6, cupulate and rather distinctly stipitate, 2–5 mm. broad, yellow or ochraceous-orange, darker when dried and paling when repeatedly soaked up, 5–6 mm. high; hymenium smooth; stem externally ribbed; exterior of sporophore provided with an irregular palisade of inflated, thick-walled cells with very narrow lumen, these apparently originating as systems of apical branchings or perhaps at times as the tips of single hyphae, often septated, and provided over their exteriors with a rough coating of spines or a definite shagginess, the walls and spinules unstained in phloxine, 8–12  $\mu$  diameter; spores elongate, often somewhat curved, hyaline, one-celled, then finally 4-celled, but one-celled spores usually predominating, smooth, 9–14  $\times$  4–5  $\mu$ .

On bark of dead standing Betula. Type collected at Ross Run, Huntingdon County, Pa., June 15, 1936. In general appearance the species is much like G. Pezisa (= G. tortus) but differs in the shorter and much more roughened cortical (peridial) cells and the broader spores. I see no special merit in recognizing the segregation of Guepiniopsis from Guepinia.

# FEMSJONIA LUTEOALBA FRIES (FIG. 9)

Until recently this fungus was unknown to America. Brasfield recently reported it from New Hampshire, Ontario, and Ohio. I would suspect that the Ohio report is an error, not in identification, but in the origin of the collection. There is too much difference between the Ohio climate and the climate under which I have seen this fungus so abundantly in Ontario and in Quebec. This opinion is supported by the apparent absence of the species from the Appalachian region, where the environmental factors would approach much more nearly those of its more northern range. Specimens I have seen in the field are more nearly a pale buff than an orange yellow as described by Brasfield, although the orange color of the

hymenium may extend over the remainder of the sporophore to some extent. The only substratum from which I have collected it is *Betula*. It was abundant in the region of Duchesnay, Quebec, in August, 1938. This is an extension of the previously known range. I have additional collections from Ontario.

# MARASMIUS MAGNISPORUS MURRILL (FIG. 2)

Collected at Laurel Run, Huntingdon County, Pa., August 11, 1937, on dead outer bark of living *Ulmus americana*. The species is none too well described, nor does it key out well in Pennington's treatment of the genus. I present, therefore, the description drawn from the 1937 collection:

Pileus 5–15 (–25) mm. broad, reviving completely after drying, convex to convex-campanulate, white, appearing tomentulose or appressed-cottony under a lens, rather delicate and appearing subgelatinous when water-soaked, drying white; context very thin, taste mild; gills adnate or somewhat decurrent, strongly interveined, forked, white, about 1 mm. broad; stem central or somewhat excentric (one specimen practically lateral), curved, at first white and minutely pubescent under a lens, at maturity somewhat blackish toward the base, 5–7 mm. long, 0.5–1 mm. thick; spores tear-shaped, *i.e.*, pip-shaped with an unusually long apiculus, smooth, hyaline,  $10-16 \times 4-5 \mu$ ; cystidia none.

Pennington uses the upward flaring of the stem as a key character. In my specimens this is not pronounced and certainly should not be used as a key character; the gills are not decidedly decurrent in all specimens; the spores run considerably larger than in the descriptions. Apparently the species is not so rare. Hard's figure 107, as *M. candidus*, is apparently this species.

# PORIA ALBOBRUNNEA ROMELL (FIGS. 4, 5, 6)

Broadly effused, sometimes for 10–20 cm. on decorticated wood, the general color pallid brown in herbarium specimens; annual, 1–3 mm. thick, separable, first developing as orbicular patches of a distinct felt-like subiculum which is gray at first but often becomes brown, and in mature specimens is visible only as a distinct marginal zone of compact tomentum 1–5 mm. or more broad, or at times practically disappearing; subiculum persisting as a soft whitish cottony layer scarcely visible to the unaided eye; tubes 0.5–3

mm. long, whitish or pale wood-colored within, the mouths varying from pale drab gray to avellaneous or wood brown in herbarium specimens, at first subcircular, finally more or less hexagonal, the dissepiments rather thin, sometimes slightly pubescent under a lens, very even and entire, averaging 3.5 to 6 per mm., the hymenium perhaps typically cracked with age; spores cylindric or allantoid, hyaline  $4-6\times1.5-2~\mu$ ; cystidia none; hyphae of the margin hyaline or hyaline and brown mixed, simple or sparingly branched, with very few cross walls and clamps and often these apparently absent,  $2.5-4.5~\mu$  diameter; in KOH solution sections of the hymenial region develop a sulphur-yellow color in the basidial layer and sage-green in the trama.

On decorticated wood of *Pinus monticola*. Known only from the vicinity of Priest River, Idaho. In my herbarium there are portions of four collections communicated to me by Dr. Weir many years ago. Parts of these specimens were submitted to Pilat at Prague, and he verified the determination. I also have had a specimen from Romell for comparison. Since there is no change to blackish when KOH is applied this species is not to be referred to the group of the brown Porias. It has not previously been reported from America. The fungus is associated with a brown carbonizing decay of the wood.

PENNSYLVANIA STATE COLLEGE, STATE COLLEGE, PA.

# NOTES AND BRIEF ARTICLES

#### CORRECTION

In the list of Myxomycetes from Quebec published on pages 728–729 in the November–December 1939 issue the species *Physarum aureum* Brandza and *Physarum sessile* Brandza should be omitted, and *Physarum sulphureum* Alb. & Schw. var. *sessile* should be added. The matter is more fully discussed on pages 346–348 in the May–June 1939 issue.—Robert Hagelstein.

### HETEROTHALLISM IN ASCOBOLUS GEOPHILUS

Ascobolus geophilus was first collected by the writer while a student in the University of Iowa. It was found rather abundantly on mud flats along the Iowa River, and was referred to as Ascobolus viridis. Later studies convinced the writer that it was distinct, and it was described as a new species based on material collected in The New York Botanical Garden. It has been frequently collected since in various parts of the country. Edwin M. Betts and Samuel L. Meyer have recently taken up a study of the species and found it to be heterothallic in that they cannot produce apothecia from the germination of a single spore, but only after it has been crossed with another spore of the opposite strain. The results of this work have been published in the American Journal of Botany 26: 617–619. 1939.—F. J. Seaver.

# Fungi of the Duke Forest

Duke University is unusually fortunate in having a large tract of woodland, comprising more than 3000 acres, just outside their door and, in fact, almost surrounding the University campus, which constitutes an outdoor laboratory for the study of practical forestry and allied subjects. Dr. Frederick A. Wolf and collaborators have taken advantage of this opportunity to conduct studies in forest

pathology and forest mycology. Bulletin 2 of Duke University School of Forestry consists of a record of all the fungi collected in Duke Forest over a period of six years. The Bulletin is thoroughly illustrated and consists of 122 pages, comprising both an index to the fungi collected and a host index, and will be found extremely useful to both mycologists and foresters.—Fred J. Seaver.

In a collecting trip through Florida and the adjoining states during the winter of 1939, I collected a rust on Oxalis Martiana Zucc., at Brunswick, Georgia. It was identified as Puccinia Oxalidis (Lev.) Dietel & Ellis. In the Manual of the Rusts in United States and Canada the range for this rust is given as southern Florida, southern Louisiana, New Mexico, Texas and Mexico. This collection extends the range farther north. The identification of the rust was checked by Dr. F. D. Kern of Pennsylvania State College.—David R. Sumstine.

# DISTRIBUTION OF A SLIME-MOLD

A noteworthy example of plant distribution occurs in the case of *Diachea miyazakiensis* Emoto. It is probably superfluous to say that this organism is one of the slime-molds technically called Myxomycetes, a word meaning mucous-mushrooms, and by other authorities Mycetozoa, literally mushroom-animals because in pursuit of food they act like animals, while in their reproduction by spores they might be taken for minute puff-balls, many of them very attractive in form and color.

Japan must have been diligently searched for Myxos seeing that by Emoto's count it was in 1934 the home of 234 species, while by the writer's counting Ontario with two and a half times the area of Japan had a record of 154 species, the United States 281 species and the world at large 373 species. In spite of careful searching the *Diachea* mentioned was not recorded until 1935 anywhere else in the world than in a locality near Tokio.

Last year Mr. Eli Davis picked up a Myxo near London, Ont., and this year another near Acton, Ont., both of which on recent

examination prove to have the same singular capillitial structure and other features of Y. Emoto's *Diachea*. The two Ontario localities are 91 miles apart, and both over 9,000 miles west or over 13,000 miles east from the Japan locality.

It will pass without argument that the species must have originated in a locality somewhere; and in generation after generation has either crossed or skirted around the Atlantic or the Pacific Ocean. The reader is invited to exercise his imagination upon the time that has elapsed since the trek began, or the miles traversed, and marvel that the microscopist cannot find, after an undoubtedly long separation in time and space, any discrepancy between Emoto's presumably good description and the fungus features of the Ontario Myxo which he sees under the microscope.

In his interesting book on Bats, G. M. Allen states that fossil remains of perfectly good bats date back to Eocene times and that as a distinct order of mammals they have continued through the intervening sixty million years to the present day. Myxos could thrive in an environment much more primitive than bats. It is hardly conceivable that a complete fossil of a slime-mold of Eocene date can be in existence, but it is quite conceivable that slime-molds in considerable variety of form and color existed before bats developed the wonderful mechanism enabling them to take their flying food in the air. We can therefore reasonably allow *Diachea miyazakiensis* 60,000,000 years or possibly twice that period to move from the place of origin to reach Japan and Canada.—John Dearness.

# TAPHRINA CARVERI RECENTLY DISCOVERED IN MISSOURI (WITH 1 FIGURE)

A specimen of *Taphrina* on silver or white maple (*Acer sac-charinum* L.) collected at Lutesville, Bollinger Co., on May 23, 1939, by Mr. Linder Englehart, was recently received from Prof. W. E. Maneval, of the University of Missouri. A critical examination of the specimen shows that the species concerned is *Taphrina Carveri* Jenkins <sup>1</sup> recently described on this kind of maple.

<sup>&</sup>lt;sup>1</sup> Jenkins, A. E. New species of *Taphrina* on red maple and on silver maple. Jour. Wash. Acad. Sci. 29: 222-230. 1939.

The specimen just cited is of particular interest since it represents not only an additional new State for the distribution of this fungus, but also it is the first observation of this species in the field since 1897. Moreover, as cited elsewhere, only three previous gather-



Fig. 1. Taphrina Carveri on Acer saccharinum. X 500.

ings of the fungus are known, viz., Ontario, 1893, and Alabama and Michigan, 1897. In connection with the distribution of the fungus in Missouri, it may be recalled that the young trees on which Dr. G. W. Carver discovered the disease in Alabama were said to be from a nursery in the neighboring State of Iowa.<sup>2</sup> The photograph of *T. Carveri* here shown is from the type specimen, which is the gathering from Michigan.—Anna E. Jenkins.

#### OTHER POISONINGS WITH CLITOCYBE ILLUDENS

An account of one case of poisoning from the above named fungus was recorded in Mycologia 31: 110. Recently a second case has come to our attention involving the poisoning of three individuals.

On September 27, 1939, a fungus referred to the writer by the Microanalyst of the Department of Health in New York City was identified as our old offender, *Clitocybe illudens*. The following detailed report on the case was later received:

"The mushrooms were picked on Sunday morning, Sept. 17, 1939, by Mr. F. an Italian resident of the Bronx, at Kensico Dam. He shared half of them, about 3 pounds, with Mr. A., his tenant. Mrs. A. prepared them for supper at about 6 P.M. Mr. and Mrs. A. consumed but a few spoonfuls because the taste was not as it should be.

<sup>&</sup>lt;sup>2</sup> Loc. cit. See footnote 1.

"On Monday, Sept. 18, 1939, Mrs. A. took sick at 8:30 A.M., and Mr. A. at about 9:00 A.M. They vomited, had diarrhea, and were in a weak condition. A physician was called in and they were both taken to a hospital. Mr. A. was sent home as his case was not a severe one. However Mrs. A. was kept hospitalized until Sept. 20, 1939, and then released.

"Mr. F. who had intended to eat his mushrooms for lunch on Monday, Sept. 18, 1939, was informed of the sickness of Mr. and Mrs. A. But he doubted that the mushrooms were the cause, and as an experiment he tried three and consumed them. He vomited within five minutes and then took a large glass of epsom salts. He required no medical attention."

Among the mildly poisonous mushrooms which would include those which do not cause death, although they may bring about severe illness of longer or shorter duration, *Clitocybe illudens* seems to be one of the chief offenders. The reason doubtless lies in the fact that the fungus occurs in such profusion, is so beautifully colored, and looks so good, it is not surprising that unsophisticated collectors should want to feast upon it, and as McIlvaine has aptly expressed it "turn from it with a regret that lingers." May we add that it is much better to have this regret before eating than after, since the after regrets are likely to linger even longer, as indicated by the above experiences.

These records are published as a warning to over-enthusiastic mushroom collectors, not to allow their appetites to triumph over their better judgment in selecting forms to be used as food. "When in doubt throw it out" is a good slogan to be followed by either the amateur or professional mycophagist.—F. J. Seaver.

#### TYROMYCES GRAMINICOLA

Stewardson Brown and N. L. Britton collected a polypore in a clump of grass near Harrington Sound, Bermuda, in 1912, which Dr. Murrill (Tropical Polypores 21. 1915.) described as a new species under the name *Tyromyces graminicola*. Dr. Murrill suggested that the host might be a species of *Sporobolus*. So far as known this is the only collection of this species until twenty-six years later in 1938, when Seaver and Waterston found it again

near the Lighthouse on stump of pampas grass, Cortuderia argentea (Nees) Stapf. A third collection was made by Mr. Waterston in November, 1939, on a clump of grass under trees in the grounds of the Public Buildings, Hamilton. So far the species is not known outside of Bermuda, but it is probable that it might be found in Florida.—DAVID R. SUMSTINE.

#### FURTHER NOTES ON DOUBLE COVER-GLASS MOUNTS

The double cover-glass mount described by Diehl<sup>1</sup> should be more generally used for mounting fungi, algae, and other non-embedded microscopic material than it now seems to be. Mounts are made quickly, easily, and are relatively permanent.

The reason for its present limited use may be due to the fact that Diehl confined his explanation wholly to the manner of sealing and without further directions it is difficult to procure a mounting fluid that is compatible with the xylol in the balsam. A beginner, instead of procuring a perfectly clear mount, is likely to be disgusted with the milky-white opaque slide that results when water mixes with xylol.

A number of mounting fluids were tried in an attempt to overcome this difficulty. The first material was glycerine jelly, which hardens and thus does not intermingle with the fresh balsam. But glycerine jelly proved unsatisfactory for so many of the mounts that it was discarded. Lacto-phenol was tried with even less success. It causes hyaline conidia later to show color, and destroys the sharpness of outline which is so much desired when studying colorless fungi.

Finally B. O. Dodge recommended Shear's mounting fluid and outlined a general method of procedure. These directions, with further ideas copied from the systems used by David Linder of Harvard and W. G. Solheim of Wyoming, are the basis for the following recipe which is now being used:

1. Use of a No. 0, 22 mm. and a No. 2, 12 mm. cover glass. An 18 mm. cover glass may be substituted for the larger cover glass if desired.

<sup>&</sup>lt;sup>1</sup> Diehl, W. W. An improved method for sealing microscopic mounts. Science **69**: 276. 1929.

2. Fungi or algae may be mounted entire. Sections of host tissue are cut with a razor, or bits of leaf macerated in heated KOH (5 per cent solution). In the last case, the material is rinsed in water and then heated in Shear's mounting fluid which consists of:

2 per cent potassium acetate (in water)	300 cc.
glycerine	
95 per cent alcohol	

- 3. The material is placed in a drop of Shear's mounting fluid on the 12 mm. cover glass. Care must be taken to orient the sections or macerations so that the fungous or algal parts will be correct for examination when the slide is finished. In mounting fungi it is desirable to add additional scrapings of spores that may have been lost in the maceration process. The mount is heated carefully over a microburner until most of the liquid has evaporated.
- 4. Place drop of pure glycerine on mount and heat slightly again.

  This is very important, for glycerine takes up water readily, and if not heated will produce a milky opaque film.
- 5. Turn the 12 mm. cover glass with the material and heated glycerine upside down onto the 22 mm. cover glass. Press down firmly. Wipe away all excess glycerine from margin of smaller cover glass.
- 6. Place a generous drop of medium heavy balsam on a microscope slide. Heat balsam gently, then place cover glasses with the 12 mm. one underneath onto it. After the balsam has spread far enough to seal the glycerine, the whole mount can be pressed down until the balsam exudes slightly from the edge of the larger cover glass.

This method of mounting has served in an excellent manner for mounting types of *Cercospora* and *Meliola*, and for the study of *Venturia inaequalis*. It also has been employed by algologists, and by teachers, who wished to have permanent slides of stomatal arrangement on leaf tissue.—Charles Chupp.

#### A New Cercospora from Oklahoma

In August and September of 1939, a species of *Cercospora* causing a serious leaf-spot of the leguminous plant, *Laburnum* anagyroides Medic., was collected in the gardens of the Agricultural and Mechanical College at Stillwater, Oklahoma. A brief search of the literature failed to disclose any species of *Cercospora* affecting this host. Specimens were sent to Dr. C. C. Chupp, who concluded that the fungus was undescribed. At his suggestion the writer offers the following description and name for the new species:

#### Cercospora Laburni sp. nov.

Maculae suborbiculares vel angularibus, 1–5 mm. diametro, cinereis, marginibus angustis atrorubrobrunneis; fungus stratum amphigenum; stromatis levis vel 50  $\mu$  crassis; plerumque in dense fasciculatis, saepe coremoideis, in masse nigeris, singulatim dilute olivaceo-brunneis, uniformis in coloris et latitutinis, parce septatis, non-ramosis, nonnumquam semel vel bis geniculatis, ad apices subtruncatis, 4–6  $\times$  20–125  $\mu$ ; conidiis hyalinis, acicularis, rectis vel nonnihil curvatis, septis inconspicuis, ad bases truncatis, ad apices acutis vel subacutis, 2–3.5  $\times$  20–110  $\mu$ .

Hab. in foliis Laburnum anagyroides.

Leaf lesions subcircular to angular, inclined to coalesce, 1 to 8 mm. in length, gray to white center with a dark reddish-brown, narrow margin; fruiting amphigenous; stroma slight to  $50\,\mu$  in width; fascicles mostly dense, often coremoid; conidiophores dark in mass, singly pale olivaceous-brown, uniform in color and width, sparingly septate, not branched, sometimes one or rarely twice geniculate, large spore scar at subtruncate tip,  $4-6\times20-125\,\mu$ ; conidia hyaline, acicular, straight to slightly curved, septa indistinct, base truncate, tip acute to subacute,  $2-3.5\times20-110\,\mu$ .

Hab.: On leaves of *Laburnum anagyroides* in Stillwater, Oklahoma, August-September, 1939.

Type: In the herbarium of the Department of Plant Pathology. Cornell University, No. 28932.—W. WINFIELD RAY.

### OVERWINTERED GIANT PUFF-BALLS IN ALBERTA

(WITH 1 FIGURE)

In May, 1938, giant puff-balls, Calvatia gigantea (Batsch) Fries, were found at Edmonton, Alberta, on a north-facing slope domi-

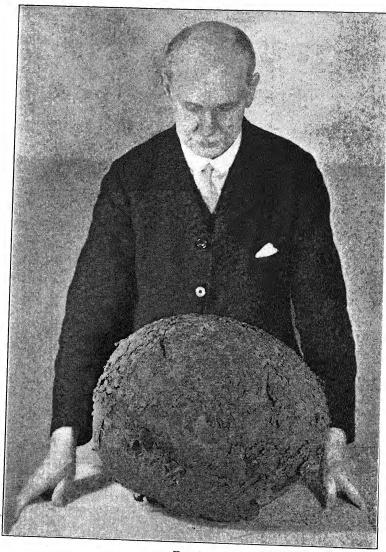


Fig. 1.

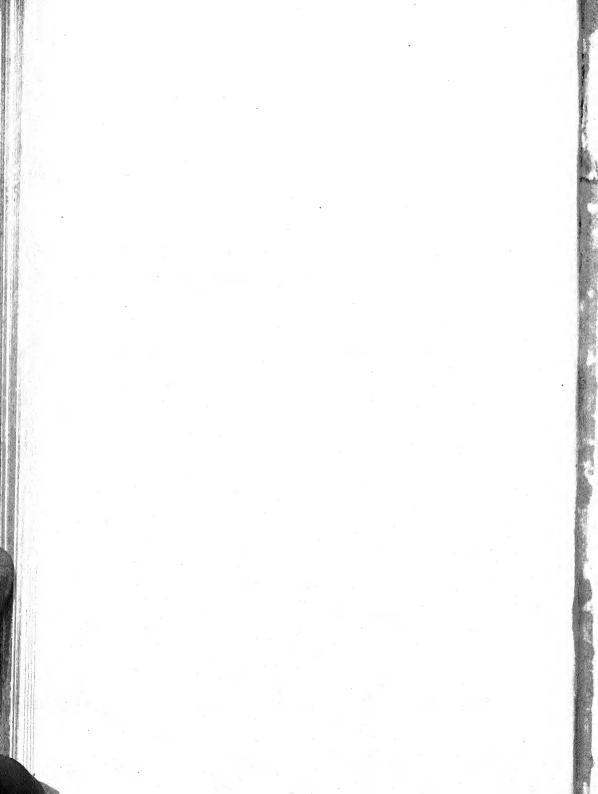
nated by grasses, shrubs and weeds. The largest of these puff-balls measured approximately 13 inches in height, 14 inches in diameter and 4 feet in circumference. Although undoubtedly fully matured the previous autumn, they were still in a good state of preservation when found on May 16th, their peridia being only

slightly broken and the spore masses mainly intact. The snow which covered them during the greater part of the winter disappeared in late March or early April, after which they were exposed to winds and, in early May, to heavy rains. Considerable protection against the elements was afforded by shrubs and by dead grass (*Calamagrostis*, *Bromus* and *Poa*) and nettles (*Urtica gracilis*) amongst which the puff-balls occurred.

On March 24th, 1939, the same area provided another collection of puff-balls most of which had overwintered in good condition. The largest of these (Fig. 1 1) measured 14 inches high, 14 inches wide, 16\% inches long and 50 inches in circumference, and weighed approximately 715 gms. after air-drying in the laboratory. At the time of collection, this puff-ball was water-soaked, the surrounding snow having only recently melted. In the laboratory the weight became more or less constant after sixteen days, fluctuating between 708 and 722 gms. and varying strikingly with the relative humidity of the room. Perhaps a very sensitive hygroscope might be made out of puff-ball gleba or capillitium system. The characters of the peridium show clearly in the photograph, especially the thin, fragile structure of the outer peridium which peels off in small, irregular patches. Buller 2 calculated that a giant puff-ball weighing 232 gms. contained about 7,000,000,000,000 spores. Therefore it may be estimated that our specimen, weighing 715 gms. contains over 20,000,000,000,000 spores.—E. H. Moss.

<sup>&</sup>lt;sup>1</sup> Professor A. H. R. Buller, who was a visitor at the University of Alberta shortly after the puff-ball was found, appeared in this photograph at the writer's request.

<sup>&</sup>lt;sup>2</sup> Researches on Fungi, I, p. 85, 1909.



# **MYCOLOGIA**

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# TWO CASES OF HAPLO-LETHAL DEFI-CIENCY IN USTILAGO BULLATA OPERATIVE AGAINST SAPROPHYTISM <sup>1</sup>

George W. Fischer

(WITH 4 FIGURES)

The smut fungi have been considered as incompletely facultative saprophytes, since in the majority of cases the haploid mycelium and sporidia have been found to be the only stage of these organisms capable of a saprophytic existence, while the dikaryon mycelium is obligately parasitic. Ordinarily no difficulty is experienced in culturing the smut fungi, and the literature shows that many species have been successfully grown on artificial media, these cultures usually being represented by pedigreed haplonts of two or more sexes, depending upon the species concerned. However, during the course of extensive cultural studies of *Ustilago bullata* Berk.<sup>2</sup> the writer has encountered a phenomenon which apparently is unparalleled in the records of previous studies of the smut fungi.

<sup>1</sup> Grass disease investigations of the Division of Forage Crops and Diseases, Bureau of Plant Industry, U. S. Department of Agriculture, in cooperation with the Soil Conservation Service, Section of Nurseries, and the Divisions of Plant Pathology and Agronomy of the Washington State College Agricultural Experiment Station.

<sup>2</sup> In this paper the binomial *Ustilago bullata* is used in the sense suggested by Fischer (6), to include *Ustilago bromivora* (Tul.) Fisch. von Waldh. and *U. Lorentziana* Thüm., long supposed to be confined to *Bromus* spp. and *Hordeum* spp. respectively.

[Mycologia for March-April (32: 129-273) was issued April 1, 1940]

What appears to be the effect of lethal factors has been discovered in certain monosporidial isolates in culture.

During the winter of 1937-38, a number of collections of Ustilago bullata were obtained in pure culture as pedigreed monosporidial isolates. Of 28 collections, 26 behaved in a more or less normal manner when sporidia were isolated to secure cultures, so that pedigreed cultures of opposite sex were easily obtained. Two collections, however, collections N-H and N-I (see legend, Table 1) from Elymus canadensis L. and E. sibiricus L. respectively, presented a perplexing and troublesome phenomenon. The isolation of sporidia was easily accomplished, but when these were allowed to grow into monosporidial cultures it was noticed that approximately only half of these isolates would bud and develop into cultures in the normal manner. The remaining isolates would bud a few times and then gradually come to a complete standstill, from which they never resumed growth. Even when transferred to a new hanging drop or block of agar they usually underwent no further development. Occasionally a very few bud sporidia would be produced, after which the colony would fail to develop further, and would finally disintegrate.

Since the cultures were desired for use as inoculum, the phenomenon described above became particularly exasperating when it was discovered that all of the isolates which did develop into colonies were of the same sexual phase. When the cultures were mated with each other on plain agar (Bauch's test for sex (1) (2)) absolutely no reaction followed. There were neither sporidial fusions nor infection hyphae, both of which characterize the reactions of sporidia of opposite sex when mixed on plain agar.

In the hope of obtaining cultures of opposite sex of these two collections of *Ustilago bullata*, isolations were repeatedly attempted. Thirteen vigorous monosporidial cultures of N–H, and 6 of N–I were finally obtained, but when these were paired with each other in all combinations, both within and between collections, they all proved to be of the same sex.

During the winter of 1938–39 it again became desirable to obtain pedigreed monosporidial cultures of opposite sex of certain collections of *Ustilago bullata*,—(1) those collections of which cultures had been lost during the summer months, and (2) new collections

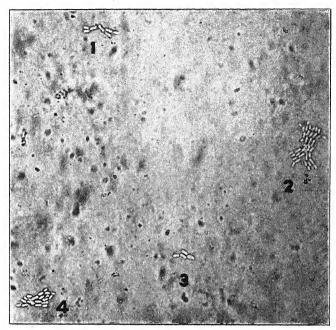


Fig. 1. Sex-linked lysis in *Ustilayo bullata* (collection N-I from *Elymus canadensis*). Four monosporidial isolates from the same promycelium 24 hours after isolation on potato-dextrose agar. Note that numbers 1 and 3 seem to be much less vigorous than numbers 2 and 4. × about 300.

added during the 1938 season. This time three additional and new collections exhibited the same phenomenon as shown by collections N-H and N-I the year before. These are as follows:

Collection		
symbol	Host	Locality
N-A3	Agropyron pauciflorum (Schwein.) Hitchc.	Soil Conservation Nurseries, Pullman, Wn.
N-L	Festuca idahoensis Elmer.	Soil Conservation Nurseries, Pullman, Wn.
M-Y	Bromus inermis Leyss.	Bozeman, Mont. (collected by L. P. Reitz)

With these collections the same difficulty was experienced, as described above, for collections N–H and N–I from *Elymus* spp. Every time two, three, or four isolates were made from the same promycelium, approximately half would fail to develop beyond budding a few times, while the remaining cultures would develop into colonies with great rapidity. Even after 24 hours growth differ-

ences between the isolates could be detected as shown in figure 1. After 48 hours the difference was even more manifest (FIG. 2) and after 72 hours the isolates possessing the growth-inhibiting factor had usually ceased growth entirely (FIG. 3). After six or seven days the normal isolates would develop into large colonies, easily visible to the naked eye, while those possessing the deficiency had not developed much if any beyond what they had attained during the first two or three days (FIG. 4).

When this phenomenon was noticed in these collections (N-A3, N-H, N-I, N-L, M-Y) during 1938-39, the question presented itself as to whether, as with N-H and N-I in 1937-38, the isolates obtained of these collections would again prove to be all of the same sex. In order to give this possibility a fair test, several isolates were obtained from each collection (only 3 from N-H since it seemed that this collection had had a fair test the previous year), until, of the five collections 29 new pedigreed monosporidial isolates

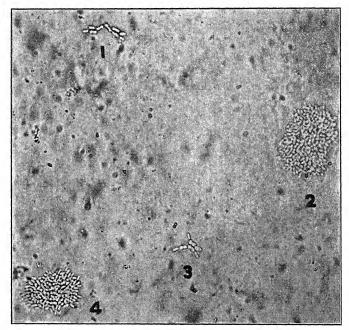


Fig. 2. Same isolates as in figure 1 but 48 hours after isolation. Numbers 1 and 3 have produced only two and three sporidia respectively.  $\times$  about 300.

had been secured. These cultures were paired with each other, both within and between collections in all possible combinations, on plain 2 per cent agar. The results of these pairings are shown in Table 1. It is seen from a glance at this table that, of the 29 isolates, all but two (N–L 64 and 71) were of the same sex. Thus cultures N–L 64 and N–L 71 gave a strong reaction (as characterized by an abundance of fusions and subsequently-produced infection hyphae) with each of the 27 other cultures. Among these latter cultures, no reaction of any kind was observed.

Since sex in the smut fungi is only a relative matter, it appeared possible that the sex reactions of these 29 isolates of *Ustilago bullata* were valid only with reference to the five collections of this species showing the haplo-lethal deficiency. Accordingly, it seemed that a further check on the 29 isolates should be made by mating them with pedigreed monosporidial isolates of other collections of *U. bullata* not possessing the deficiency, and also with other available species. Twenty-two pedigreed monosporidial cultures representing *U. nigra* Tapke, *U. bullata*, *U. Hordei* (Pers.) Kellerm. & Swingle, *U. levis* (Kellerm. & Swingle) Magn., and *U. Avenae* (Pers.) Jens.³ were paired against the 29 isolates of the collections of *U. bullata* exhibiting this growth-inhibiting factor. The results of these matings are summarized in Table 2.

The data presented in Table 2 show that the sex reaction of the 29 isolates of *Ustilago bullata* obtained when these were paired with each other is fully substantiated by the reaction obtained when the same cultures were paired with cultures of other species and with other collections of *U. bullata*. Thus, cultures N–L 64 and N–L 71 are of one sex, and the other 27 isolates are of another sex, not only with reference to each other, but also to isolates of other *Ustilago* spp., and of other collections of *U. bullata*.

Apparently, in collections N-A3, N-I, N-H, and M-Y this lethal factor is definitely sex-linked; otherwise at least a few of the 36 isolates (including 13 isolates of N-H studied in 1937-38) of these collections would have proven to be of opposite sex from the others. Since it is possible to determine positively after 24-36

<sup>&</sup>lt;sup>3</sup> The writer is indebted to Wayne Bever and C. S. Holton, Division of Cereal Crops and Diseases, for chlamydospores of *Ustilago nigra*, and for pedigreed monosporidial cultures of *U. levis* and *U. Avenae*, respectively.

Reactions of 29 Monosporidial Isolates of Ushlago bullata (Representing the Collections N-A3, N-I, N-I, N-H, and M-Y Which Exhibit a Lethal Character Inhibiting a Saprophytic Existence) When Mated with Each Other, Both Within and Between Collections TABLE 1

M-Y	111 121 132 81 91 92 101 111 113 121 131 53 64 71 81 111 121 111 121 131 71 82 91 102 112 121 132	11111	
	82	11111	1111111
	171	11111	1111111
	131	11111	1111111
H-N	121	11111	1111111
	1111	11111	1111111
	121	11111	
	111	11111	1117111
s N-L	81	11111	1111111
	71	+++++	+++++++
ECLI	64	++++	+++++++
OFF.	53	11111	1111111
DEIWEEN COLLECTIONS	131	11111	1 1 1 1 1 1 1
ਜ਼ੇ ≿ ਜ	3 121	11111	111111
7	113	11111	11111
I-N	1111	11111	11111
	10	11111	1111
	92	11111	1 1 1
	91	11:111	1.1
	2 81	11111	1
	132	11111	
3	121	1111	••
N-A3	111	111	18
	82 101	11	
	82	1	
		82 101 111 121 132 132	92 92 101 111 113 121 131
		N-A3	I-N

		CEZ-AT	,			1- X1	;					T-L	,			H-N	E			Ξ.	M-Y		
	<u>"</u>	82 101 111 121 132 81 91 92 101 111 113 121 131 53 64 71 81 111 121 111 121 131 71 82 91 102 112 121 132	121 132	81 9	1 92	101	111	13 12	1 131	53	64	7.1 8	31 1	11 1	21 111	1 12	1 13	1 71	82	91	102 1	12 1	21 1
	53									1	+1	+1	1	1	<del></del>	1	1	1	1			1	
N-L	711												-+1	-+। -+।	++    ++	⊦+, ı	++ I	++1	++1	++1	· ++;	++	++
	111												1	11	11	1-1	11	11					
H-N	111 121 131	,													1	11	111			' ' '			
-	71 82				-	-																	
M-Y	102 112 121 133																		'			1111	
	7																						1

+ = Numerocana N-A3 = Usuidago bullata from Agropyron pauciflorum N-A3 = Usuidago bullata from Agropyron pauciflorum N-I = "" " Elymus subsricus N-I = "" " Festuca idahoensis N-I = "" " Bromus canadensis "" Bromus inermis

Reactions of 29 Monosporidial Isolates of Ustilago bullata (Representing the Collections N-A3, N-I, N-L, N-H, M-Y Which Exhibit a Lethal Character Inhibiting a Saprophytic Existence), with U. migra, U. bullata, U. Hordei, U. levis and U. Avenae TABLE 2

6)	534	++++-		+11+++
4 <i>vena</i> . a.	533	1111		++
U.a.	532	++++	- +++++++	+11+++
SANL	531	11111	11111111	1++111
	914	1111	1111111	1++111
uer, c	913	+++++	++++++	+11+++
U.I.	912	+++++	-	+11+++
, ,	911	11111		1++111
f-	73	++++	++++++	+11+++
M-J U.1. U.1. U.2. U.3.	72	11111	1111111	1++111
N-E	73	+++++	++++++	+11+++
Ż	7.1	11111	1111111	++
:	54	+++++	++++++	+11+++
, Q	53	11111	1141111	1++111
Е-D	52	+++++	+++++++	+11+++
	51	11111	1111111	1++111
	94	+++++	++++++	+11+++
N-F	93	11111	1111111	1++111
Z	92	+++++	++++++	+11+++
*	91	11111	1111111	1++111
K-A	114	11111	1111111	1++111
M	113	+++++	++++++	+11+++
*		82 101 111 121 132	81 91 92 101 111 113 121 131	53 64 71 81 111 121
		N-A3	I-N	N-L

	534	+++	++++++
5	533	111	111111
U.a.	532	+++	++++++
	531	111	1111111
	914	111	111111
_;	913	+++	++++++
U.I.	912	+++	++++++
	911	111	111111
-	73	+++	++++++
M-J	72	111	111111
nrmnea) N-E	73	+++	++++++
IABLE 2 (Continued) E-D N-E	71	. 1 1 1	1111111
7	54	+++	++++++
LADLE E-D	53	111	111111
<del>-</del> ы	52	+++	++++++
	51	111	1111111
	94	+++	++++++
Į.	93	111	111111
N-F	92	+;++	++++++
	91	111	111111
V-	114	111	111111
X	113	+++	++++++
		111 121 131	71 82 91 102 112 121 132
		H-N	M-Y

Legend: + = sporidial fusions in abundance and subsequent infection hyphae - = no reaction

	cultivated barley	E-D = "Hordei, ""	" oats	11	Elymus sibiricus	A gropyron inerme	Bromus squarrosus	Agropyron pauciflorum	Elymus sibiricus	Festuca idahoensis	Elymus canadensis	Bromus inermis
	from	;	:	1.	,,	,,	,	;	"	<b>:</b> .	,,	:
CII	nigra,	Hordei,	levis,	Avenae,	bullata,	3	:	3	"	"	"	=
10 react	Ustilago	) :	3,	=	3	3	3	3	ï	3	3	;
1	K-A =	E-D =	U.I. =	U.a. =	N-F =	N-E =	M-[ =	N-A3 =	N-I =	= 7-N	= H-N	M-Y =
								~				

hours which isolates will and which will not continue development, a further check on the sex-linkage of this lethal character was made by transferring a few sporidia from both types of isolates to hanging drops of plain agar and mixing them, by means of a Chambers micro-manipulator. This was done with each collection, excepting N–L. In each case, infection hyphae resulted from such matings, although the fused sporidia could not be definitely discerned. Further proof is thus indicated that the sporidia which are incapable of developing into colonies are of one sexual phase, and the other sporidia, which can be cultured, are of the other phase.

In the case of collection N-L, in which the lethal appears not to be sex-linked, further study seemed desirable to determine if, in isolates N-L 64 and N-L 71, the factor somehow happened to segregate independently of the factor for sex, or if such independence of segregation is the rule. Accordingly from 13 promycelia 30 sporidia were isolated and their subsequent development watched. The history of these isolates is given in Table 3.

TABLE 3

History of the Behavior of 30 Pedigreed Monosporidial Isolates of Collection N-L of *Ustilago bullata* on Malt Agar

Promy-	Sporidia	Sporidia with lethal	Sporidia develop-	Sex dist	ribution
celium No.	isolated: Pedigree Nos.	factor: Pedigree Nos.	ing into colonies: Pedigree Nos.	+	_
13 14 15 16	1, 2, 3 1, 2, 3 1, 2 1, 2, 3 1, 2, 3	1 2 2 1, 3	2, 3 1, 3 1	2	3 1, 3
17 18 19	1, 2, 3 1, 2 1, 2 1, 2	1, 2 2 1, 2	1, 2, 3	1, 3	2
20 21 22 23 24 25	1, 2 1, 2 1, 2 1, 2 1, 2 1, 2 1, 2 1, 2	2 1, 2	1, 2 1, 2 1, 1	1, 2 1, 2 1	2 1
Totals	30	14	16	10	6

As seen in Table 3, of the 30 sporidia isolated, again approximately half possessed a haplo-lethal deficiency. Sixteen budded

rapidly into normal sporidial colonies, while 14 failed to develop beyond the production of a few bud sporidia. When the 16 normal isolates were paired with each other in all combinations it was found that both sexes were represented; 10 were of one sex and 6 of the other. These results are regarded as further proof that the haplo-lethal exhibited in collection N–L of *Ustilago bullata*, from *Festuca idahoensis*, is definitely not sex-linked.

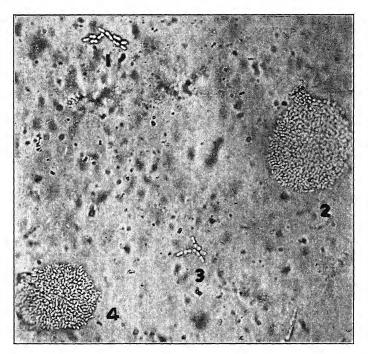


Fig. 3. Same isolates as in figures 1 and 2 but 72 hours after isolation. Numbers 1 and 3 have almost ceased growth entirely at 10 and 7 sporidia respectively, while numbers 2 and 4 each consist of hundreds of sporidia.  $\times$  about 300.

Considering that collections N-A3, N-H, N-I, and M-Y do possess a sex-linked haplo-lethal deficiency, the question arose as to whether the factor is operative in nature under field conditions. If one sex is entirely repressed, even in nature, it would be difficult to understand how infection could take place, considering that both sexes are necessary to infection.<sup>4</sup> Chlamydospore material of col-

<sup>&</sup>lt;sup>4</sup> The writer's unpublished data.

lections N-A3, N-I, and M-Y being of sufficient quantity to provide inoculum, a number of grasses were inoculated with these, seeded in the greenhouse and transplanted to the field in the spring of 1939. The results of these inoculations will be reported in detail elsewhere. It is sufficient to record here that no infection was obtained with N-A3, but high percentages of infection resulted on a number of grasses in the case of collections N-I and M-Y. It is thought the few grasses used for collection N-A3 did not include a susceptible host. At least in the case of collections N-I and M-Y the lethal factor did not operate against infection.

#### DISCUSSION

Lysis in the smut fungi, thought to be due to lethal factors, has been reported before, but apparently only in germinating F1 chlamydospores. Chilton (4) and Laskaris (7) reported the occurrence of such lysis in F1 spores of only certain combinations of monosporidial lines of Ustilago Zeae (Beckm.) Unger and of Sphacelotheca Sorghi (Link) Clint., respectively, and the phenomenon was thought to be due to a lethal factor or factors. In these cases, however, the lysis reported must have been of an entirely different nature from that reported in the present paper in that the lethal factor apparently was not operative against the saprophytic development of the haplonts, else they could not have been cultured to provide the monosporidial lines which were combined to make the crosses. The cases of lysis in the smut fungi reported by previous investigators have been represented by the abnormal germination of the chlamydospores and subsequent death of their promycelia.

Although zygotic and sporophytic lethals are common in both plants and animals, gametic and gametophytic lethals apparently are rare. Dodge (5) reported a lethal agent in cultures of *Neurospora tetrasperma*. In crosses where one of the parents possessed the lethal, half of the uninucleate f1, f2 or f3 ascospores would die after undergoing slight germination. The remaining ascospores produced mycelia of normal growth, and represented both sexes. The lethal was not, therefore, sex-linked and corresponds to the lethal exhibited in collection N–L of *Ustilago bullata* described above. Wettstein (8) recorded an instance of the operation of a

lethal in certain F1 interspecific moss hybrids where two spores of a tetrad gave rise to plants similar to the female parent, while the other two failed to develop further. Here it can only be assumed that the two lethal spores represented the male gametophytes, in which case the lethal was sex-linked. This situation would be homologous to the sex-linked lethal described herein for *U. bullata*, since the four tetraspores correspond to the four sporidia typically produced on the promycelium of many *Ustilago* spp.

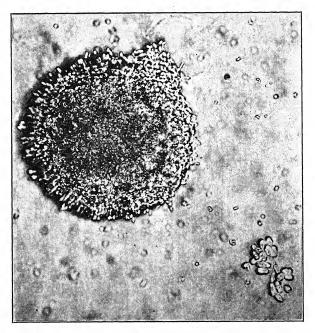


Fig. 4. Sex-linked lysis in *Ustilago bullata* (collection N-A3 from *Agropyron pauciflorum*). Development of two monosporidial isolates from the same promycelium six days after isolation on potato-dextrose agar. One isolate consists of thousands of bud sporidia, whereas the other consists of approximately only 25 sporidia. × about 450.

Lethals of pollen-tube development in F1 progeny from radiumtreated parents in *Datura* have been described by Buchholz and Blakeslee (3). One lethal expressed itself in two ways: (1) Failure of half of the pollen grains to germinate. (2) Early bursting of half the pollen tubes. Here is a case, then, of a gametophytic lethal in the seed plants. Other cases have been reported. These other instances of gametic or gametophytic lethals do not help much in explaining the present cases of haplo-lethal deficiency in *Ustilago bullata*. The writer's material had not had radium or x-ray treatment, nor was it of hybrid origin (unless representing natural hybrids which is, of course, possible). Obviously more detailed study of the genetics of these collections of *U. bullata* possessing the lethals is necessary to a more complete explanation of their expression. At present it would seem that in one instance (collection N–L) the lethal is probably borne on an odd chromosome and is independent of the factor or factors for sex. In the other four instances it seems definite that the lethal factor is somehow linked with the factor governing sex.

In conclusion it should be pointed out that possibly the haplolethal deficiencies described herein for certain collections of *Ustilago bullata* should be considered as only "semi-lethal" inasmuch as they seem to operate only against saprophytic growth and do not interfere with the normal function of paired nuclei in initiating the parasitic dikaryophase.

#### SUMMARY

Five collections of *Ustilago bullata* on *Agropyron, Bromus, Elymus*, and *Festuca* spp. were found to possess a haplo-lethal deficiency preventing saprophytic development. Approximately half of the sporidia isolated from any promycelium would develop, when isolated, into typical sporidial colonies. The other sporidia would bud several times and then gradually undergo complete lysis.

In four of the five collections this lethal appears to be definitely sex-linked. Forty-two pedigreed monosporidial isolates of these four collections proved to be all of the same sex phase. The fifth collection possesses a lethal which is segregated independently of sex factors, since both sexes were represented in the isolates not possessing the character.

Twenty-nine pedigreed monosporidial isolates of the five collections exhibiting the lethal were paired with 22 such isolates from

<sup>5</sup> Since submitting this paper for publication a recent contribution by Winge and Laustsen (Saccharomycodes Ludwigii Hansen, a balanced heterozygote. Compt. Rend. Lab. Carlsberg Ser. Phys. 22: 357–370. 1939.) has come to the writer's attention. These authors describe a phenomenon in a yeast fungus quite comparable to the lethals here described for Ustilago bullota.

Ustilago nigra, U. Hordei, U. levis, U. Avenae and of collections of U. bullata not possessing it. Both sexes were equally represented in these 22 isolates, and when paired with these, the 29 isolates from collections exhibiting the character gave the same reaction as when paired with each other. Thus, in the four collections in which the lethal factor is sex-linked, the 23 isolates representing these collections were all of the same sex, not only with reference to each other, but with reference to the 22 isolates of other collections and other species.

These haplo-lethal deficiencies operate only against saprophytic development. When chlamydospores of two of the collections were used as inoculum high percentages of infection were easily obtained, showing that both sexes operate toward parasitic development, since both are necessary to infection.

Since the lethals are exhibited by approximately half of the sporidia borne on any promycelium, it is considered that they are probably borne on odd chromosomes, in one case sex-linked and in the other independent of sex.

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# THE RUSTS OF MINAS GERAES, BRAZIL BASED ON COLLECTIONS BY A. S. MÜLLER 1

H. W. THURSTON, JR.

The following is a report on the identification of the rusts collected in Minas Geraes, Brazil, by A. S. Müller formerly of the Escola Superior de Agricultura at Vicosa.

Professor Müller was from 1928–1937 an ardent collector of fungi in this region. His Brazilian specimens, numbering about 1200, are all deposited in the Herbarium of Cornell University at Ithaca, New York. Among them there are 210 collections of rusts. While many of these represent common and well known species, it is of interest to record many comparatively rare forms and six new to science. The present list records 108 species.

The Holway collections of South American rusts, made 1919–1922, probably represent the most extensive previous collections from this region. Arthur (Proc. Am. Phil. Soc. 64. 1925) reports that 81 of the Holway specimens were secured in Minas Geraes. These as studied in part by Arthur and later completed by Jackson yielded 50 species from this Brazilian state. About half of these have been duplicated in the Müller collections.

Without any attempt to make a complete search of the literature for reports of other rusts in Minas Geraes, we have on the basis of these two lists approximately 130 species known from this region. Without doubt, this figure represents a very incomplete picture of the rust flora of so large and varied an area. It should be pointed out however, that only through long continued accumulation of such information as is here presented, can we hope to arrive at a fuller understanding of the factors that determine the distribution and ecology of parasitic fungi.

The writer wishes to acknowledge his indebtedness to Doctor F. D. Kern who has aided him generously with many determina-

<sup>&</sup>lt;sup>1</sup> Contribution from the Department of Botany, The Pennsylvania State College, no. 127.

tions. The help of many colleagues who have responded promptly to calls for aid, especially in determination of the hosts, is also gratefully acknowledged.

AECIDIUM BRASILIENSE Dietel, Hedwigia 36: 35. 1897. On *Cordia ecalyculata* Vell., Vicosa (Teixeras), Oct. 26, 1934, 854.

AECIDIUM CIRCINATUM Wint. Hedwigia 23: 168. 1884.

On Bignoniaceae indet. possibly Stenolobium sp., Maria da Fi, Dec. 29, 1930, 226.

Of the several aecia described on Bignoniaceae, this species with the walls of the aeciospores thicker above appears to be quite distinct. While we have had no opportunity to compare our specimen with the type it is placed here with considerable confidence.

AECIDIUM LINDAVIANUM Sydow, Monog. Ured. 4: 129. 1923. On Cordia aff. alba (Jacq.) R. & S., Vicosa, Nov. 14, 1929, 20.

The type of this species which was described from Peru has not been available, but it seems to be distinct from other aecia on *Cordia*, the spores being quite small,  $15-16 \times 18-21 \,\mu$ . This constitutes the first report of the species for Brazil.

# Aecidium Mabeae sp. nov.

Pycnidiis epiphyllis, paucis, in greges parvos usque 1 mm. diam. aggregatis, conspicuis, dein nigrescentibus, subepidermicis, globosis,  $80-100~\mu$  diam. Aecidiis hypophyllis, in maculis decoloratis 2–5 mm. diam. dispositis, cupulatis, profunde insidentibus, 0.1-0.2 mm. diam.; peridio albido, margine erecto; cellulis peridialibus rhomboideis,  $26-32~\mu$  longis, subimbricatis, pariete exteriore levi, ca.  $3~\mu$  cr. interiore  $4-6~\mu$ , striato, valde tuberculato-verrucoso; aecidiosporis late ellipsoideis vel oblongis,  $20-26~\times~27-35~\mu$ ; tunica hyalina,  $1.5-2~\mu$ , plerumque ad apicem incrassata,  $5-7~\mu$ , promimenter verrucosa.

On Mabea brasiliensis Muel.-Arg., Vicosa, April 1, 1933, 438.

Of the numerous aecia on the family Euphorbiaceae there appears to be only one, *Aecidium Maprouneae* P. Henn. with spores thicker above. Our specimen on *Mabea* has spores thicker above, but not so thick as has been described for *A. Maprouneae*. In addition the aeciospores of our specimen are different in shape,

being less oblong. We have had no specimen of A. Maprouneae for comparison, but believe that the rust on Mabea is distinct.

## Aecidium Mülleri sp. nov.

Pycniis epiphyllis, numerosis, in greges 2–7 mm. diam., in maculis decoloratis collectis, dein nigrescentibus, subepidermicis, non profunde insidentibus, conicis, magnis,  $200-250 \mu$  latis,  $100-130 \mu$  altis; paraphysibus incognitis.

Aecidiis hypophyllis, plus minusve in greges 2–8 mm. diam. in maculis decoloratis circinatim dispositis, cylindraceis, 0.2–0.3 mm. diam., peridio albido, margine eroso, plus minusve erecto; cellulis peridialibus rhomboideis, 28–32  $\mu$  longis, subimbricatis, pariete exteriore leve, 3–4  $\mu$  cr., interiore 5–6  $\mu$ , tuberculato-verrucoso; aecidiosporis late ellipsoideis, 13–16  $\times$  16–23  $\mu$ ; tunica hyalina, tenui, ca. 1  $\mu$  cr., subtillissime verrucosa.

On Nectandra amara Nees., Vicosa, Dec. 3, 1929, 39.

This Aecidium is quite distinct from A. Nectandrae Jackson & Holway, which has larger spores that are thickened at the apex.

AECIDIUM TOURNEFORTIAE P. Henn. Hedwigia 34: 338. 1895. On *Tournefortia* sp., Vicosa, Aug. 30, 1934, 846.

AECIDIUM XANTHOXYLINUM Speg. Rev. Argent. Hist. Nat. Buenos Aires 1: 400. 1891.

On Xanthoxylum sp., Vicosa, May 2, 1931, 265.

Dictyoloma peruviana Planch., Vicosa, Feb. 17, 1934, 729.

These specimens are referred to this species without any authentic material for comparison. This rust has not been reported before on *Dictyoloma* which is closely related to *Xanthoxylum*. Both are genera of the family Rutaceae. The small spores 16–22  $\mu$  which appear smooth, seem to be quite distinct from any other rust on the order *Rutales*, though similar except for size to *A. Xanthoxyli* Peck, which is known in North America.

BITZEA INGAE (Sydow) Mains, Mycologia 31: 38. 1939. Maravalia Ingae Sydow, Mycologia 17: 257. 1925. Ravenelia Ingae (P. Henn.) Arth. N. Am. Flora 7: 132. 1907. On Inga edulis Mart., Uberaba, May 19, 1936, 1072.

Inga sp., Vicosa, Jan. 20, 1935, 878.

The name proposed by Mains is being used for this species. For a complete account of the synonomy involved, see his account (Mycologia 31: 33–42. 1939).

- THURSTON: THE RUSTS OF MINAS GERAES, BRAZIL 293
- CEROTELIUM DESMIUM (Berk. & Br.) Arth. N. Am. Flora 7: 698, 1925.
- On Gossypium brasiliense Macfad., Vicosa, Feb. 19, 1930, 134. Gossypium sp., Bello Horizonte, July 14, 1935, 954.
- CEROTELIUM FICI (Cast.) Arth. Bull. Torrey Club 44: 509. 1917 On Ficus carica L., Vicosa, Oct. 13, 1929, 52.
- Cerotelium malvicolum (Speg.) Diet. in E. & P. Nat. Pfl. II, 6: 57. 1928.
- On Pavonia spinifer Cav., Vicosa, May 25, 1934, II & III, 804.
- Coleosporium Elephantopodis (Schw.) Thüm. Myc. Univ. 953. 1878.
- On *Elephantopus mollis* HBK., Vicosa, Nov. 14, 1929, 22; June 3, 1933, 563.
- COLEOSPORIUM IPOMOEAE (Schw.) Burr. Bull. III. Lab. Nat. Hist. 2: 217. 1885.
- On Ipomoea cairica Sweet, Ouro Preto, Dec. 29, 1929, 79.
- Desmella Aneimiae (P. Henn.) Sydow, Ann. Myc. 16: 241. 1918.
- On Anemia sp., Vicosa, June 3, 1933, 566.
- DIDYMOPSORA SOLANI-ARGENTEI (P. Henn.) Dietel, Hedwigia 38: 254. 1899.
- On Solanum Swartsianum R. & S., Vicosa, April 1, 1933, 445. Known only from Brazil.

# Endophylloides Degueliae sp. nov.

Pycnidiis non visis.

Teleutosoris hypophyllis, in maculis hypertrophicis 3–20 mm. diam. aggregatis, profunde insidentibus, peridio non visibili; sporas in columnas, siccas corneas protrudentibus; columnis 0.3–0.4 mm. diam.  $\times$  0.4–0.6 mm.; teleutosporis catenulatis, angulato-ellipsoidiis 18–21  $\times$  26–36  $\mu$ , tunica hyalina. 2–3  $\mu$  cr. ad apicem incrassata usque 7  $\mu$ , subtillisime verrucosa.

On Deguelia furfuracea (St. Hil.) Benth. & Hook. Uberlandia, May 18, 1936, 1065.

This rust has certain superficial characters like an aecidium. The absence of a peridium together with the fact that the spores form quite definite waxy or horny columns do not indicate its relationship with the form genus *Aecidium*. There are very definite characteristics of the genus *Endophylloides* as set up by Whetzel & Olive. To make the reference to this genus unquestionable it should be known how the spores germinate. While this is not known the structural characters, on which we usually rely, seem sufficient to warrant reference to this genus.

Keuhneola Loesneriana (P. Henn.) Jackson & Holway, Mycologia 23: 105. 1931.

On Rubus sp. Vicosa, Mar. 24, 1933, 420; Feb. 4, 1934, 688.

PHAKOPSORA CROTALARIAE (Dietel) Arth. Bull. Torrey Club 44: 509. 1917.

On Crotalaria stricta (DC.), Vicosa, April 2, 1936, 1044.

Pнакорsora crotonicola (Р. Henn.) К.Т.W. Monog. Univ. Puerto Rico Series B, No. 2: 271. 1934.

Phakopsora argentinensis Arth. 1917.

On Croton cf. compressus Lam., Vicosa, July 3, 1933, 568.

This specimen bears uredinia only. The spores seem a trifle large for this species but are occasionally thickened above. We are following Jackson (Mycologia 23: 465) and Kern, Thurston and Whetzel (Monog. Univ. Puerto Rico Series B, No. 2: 271. 1934) in considering this species distinct from *P. Crotonis* (Cooke) Arth.

Phragmidium disciflorum (Tode) James. Contr. U. S. Nat. Herb. 3: 276. 1895.

On Rosa (Vich's Caprice), Vicosa, Aug. 27, 1934, 834.

Müller's specimen no. 33, collected in 1929 also at Vicosa, is undoubtedly the same species although no telia were present, making the identification less certain.

THURSTON: THE RUSTS OF MINAS GERAES, BRAZIL 295

Prospodium impolitum Jackson & Holway, Mycologia 24: 90. 1932.

On Bignoniaceae (undet.), II & III, Vicosa, July 2, 1934, 810.

It is to be regretted that a more specific host identification is impossible. All previous localities for the species are in Sao Paulo, Brazil.

Prospodium tecomicola (Speg.) Jackson & Holway, Mycologia 24: 94. 1932.

On Tecoma sp., Lavras, J. Deslandes 986.

This species has been reported from Sao Paulo, Brazil, by Jackson (Mycologia 24: 94. 1932). Dr. G. B. Cummins has suggested in a letter that *Prospodium concinnum* described from Venezuela by Sydow is probably identical.

PROSPODIUM TUBERCULATUM (Speg.) Arth. N. Am. Flora 7: 161. 1912.

On Lantana camara, var. aculeata (L.) Moldenke, II, Ita, Aug. 23, 1932, 361.

Lantana camara L. II, Vicosa, Feb. 17, 1934, 742.

# Prospodium Wulffiae sp. nov.

Uredosoris non visis; uredosporis teleutosoris immixtis, late ellipsoideis vel globosis,  $19-20\times 21-26\,\mu$ ; tunica pallida brunneo-flavida,  $1.5\,\mu$  cr., moderate echinulata; poris 2, aequatorialibus.

Teleutosoris hypophyllis, sparsis vel gregariis, minutis, rotundatis, ca 1 mm. cr., mox nudis, pulverulentis, cacao-bruneis, epidermide rupta visibili; paraphysibus soro circumdantibus, incurvatis, altitudini sorae aequante, tunica dilutissime bruneola, leve; teleutosporis late ellipsoideis,  $22-26 \times 32-39 \,\mu$ , supra et infra rotundatis; tunica obscure castaneo-brunnea, laminata, 2.5-3.5  $\mu$  cr., lamina exteriore gelatinosa non conspicua, prominenter papillis conicis verrucosa, ad apicem incrassata usque 6-7  $\mu$ , poro cellulae superioris apicale, inferioris basali, super poros in umbonem pallidiorem incrassata; pedicello hyalino, sporis breviore, infra singulo orbi appendiculato.

On Wulffia maculata (Ker.) DC., Vicosa, April 12, 1933, 456.

It is not easy to decide whether this species should be referred to *Puccinia* or to *Prospodium*. The characters of the teliospores such as the laminate walls, the pores, and the appendages on the

pedicels are typical for *Prospodium*. There are incurved paraphyses and the urediniospore markings and pores agree also with *Prospodium*. Thus far *Prospodium* has been reported on *Bignoniaceae* and *Verbenaceae* with a single exception of a species on *Sapindaceae*. This host is a *Composite* but it would seem that the structural characters warrant placing the species in the genus *Prospodium*.

Puccinia Acanthospermi P. Henn. Hedwigia 41: 296. 1902. On *Acanthospermum australe* (Loefl.) Kuntze, Vicosa, Dec. 23, 1933, 667.

Originally described on A. xanthioides from Venezuela, this species has been reported previously from Rio de Janeiro and São Paulo in Brazil.

Puccinia Allii (DC.) Rud. Linnaea 1: 392. 1829. On Allium sativum L., Vicosa, II & III, Aug. 8, 1935, 983.

The compact telial sori with numerous paraphyses have led to the use of the name, *P. Allii* although some taxonomists have considered this species to be a synonym of *P. Porri* (Sow.) Wint.

I have seen no report of either species from South America.

Puccinia augustatoides R. E. Stone, Bull. Torrey Club 36: 549. 1909.

On Rynchospora sp., Vicosa, Feb. 6, 1930, 120.

This specimen bears telia as well as uredinia which places the collection with considerable certainty as *P. augustatoides*. Previous collections consisting of uredinia only have usually been referred to *Uromyces Rhyncosporae* Ellis. (See Jackson, Mycologia 18:147. 1926.)

Puccinia Arechavelatae Speg. Anal. Soc. Ci. Argent. 12: 67. 1881.

On Cardiospermum grandiflorum Sw., Ana Florencia, July 21, 1933, 631.

Cardiospermum Halicacabum L., Vicosa, April 24, 1930, 167. Serjania sp., Vicosa, Feb. 16, 1930, 129; Dec. 14, 1933, 652;

THURSTON: THE RUSTS OF MINAS GERAES, BRAZIL 297 Sagoa Santa, July 16, 1935, 960; Curvello, Mar. 1, 1936, 1007.

Puccinia atra Dietel & Holway; Holway, Bot. Gaz. 24: 29. 1897.

On Valota insularis (L.) Chase., Vicosa, Dec. 30, 1929, 82.

Puccinia Bambusarum (P. Henn.) Arth. Bot. Gaz. 65: 467. 1918.

On Olyra micrantha H.B.K., Vicosa, Dec. 7, 1933, 645.

Puccinia Cameliae (Mayor) Arth. Mycologia 7: 227. 1915. On Setaria scandens Schrad., Vicosa, Mar. 30, 1933, 433.

Puccinia Cannae (Wint.) P. Henn. Hedwigia **41**: 105. 1902. On *Canna* sp., II, Vicosa, Mar. 20, 1932, *321*. *Canna indica*, Vicosa, Feb. 18, 1935, *872*.

Puccinia Capsici Mayor, Mém. Soc. Neuch. Sci. Nat. 5: 501. 1913.

On Capsicum sp., Vicosa, Nov. 14, 1930, 230.

The small teliospores of this specimen agree very well with *Puccinia Capsici*. Dr. H. L. Mason, of the University of California, has examined the specimen and writes that the host is probably an undescribed species of *Capsicum*.

Puccinia Cenchri Dietel & Holway, Bot. Gaz. 24: 28. 1897. On Cenchrus echinatus L., Uberlandia, May 18, 1936, 1066. Cenchrus sp., Rio Brancho, July 31, 1934, II & III, 827.

Puccinia crassipes Berk. & Curt.; Berk. Grevillea 3: 54. 1874. On *Ipomoea* sp., Vicosa, June 12, 1931, I & III, 274; April 16, 1933, I & III, 461.

Specimen 274 bears abundant telia which are considered rare in this species. Mains (Carnegie Inst. Wash. Pub. 461, 102. 1935) suggests that the aecia may be repeating aecia. We can confirm his observations concerning the absence of pycnia.

Puccinia Cynodontis Lacroix, in Desmaz. Pl. Crypt. II 655. 1859.

On Capriola Dactylon (L.) Kuntze, Vicosa, May 15, 1930, 175.

Puccinia elongata Speg. Anal. Soc. Ci. Argent. 9: 168. 1880.
Aecidium Verbenae Speg. Anal. Soc. Ci. Argent. 9: 174. 1880.
On Verbena brasiliense Vell., I, III, Vicosa, July 6, 1935, 944; I only, Vicosa, Oct. 4, 1929, 1.

That Puccinia elongata and Aecidium Verbenae are stages of one and the same fungus seems indisputable from a study of Müller's specimen 944, which bears abundant telia arising within and around the aecia. The telia are compact and by themselves might certainly suggest a short cycled species. Our study indicates, however, that Spegazzini's early surmise as to the identity of these two forms was correct. The aecial stage has been the one most frequently collected. Pycnia are lacking and the suggestion is offered that the aecia may be repeating aecia. This species would seem to present a parallel case to that of P. crassipes noted above.

Puccinia Eupatorii Dietel, Hedwigia 36: 32. 1897.

On Eupatorium squalidum DC., II & III, Lagoa Santa, July 16, 1935, 957.

Eupatorium sp., Vicosa, Nov. 2, 1935, 997.

No. 997 bears uredinia only but seems without doubt to belong here.

Puccinia evadens Hark. Bull. Calif. Acad. 1: 34. 1884. On *Baccharis* sp., Vicosa, June 3, 1933, *564*.

Jackson (Mycologia 24: 143. 1932) has suggested that there is some doubt as to the specific limits of *P. evadens*. Our specimen agrees well with Holway's specimens from Minas Geraes which have been referred to this species.

Puccinia flaccida Berk. & Br. Jour. Linn. Soc. 14: 91. 1873. On Echinochloa Crus-galli Beauv., Bello Horizonte, Dec. 23, 1929, 78; II & III, Vicosa, April 4, 1930, 163.

THURSTON: THE RUSTS OF MINAS GERAES, BRAZIL 299

Puccinia Gnaphalii (Speg.) P. Henn. Hedwigia Beibl. 41: 66. 1902.

On Gnaphalium purpureum L., Vicosa, June 20, 1933, II, 621.

PUCCINIA GOUANIAE Holway, Ann. Myc. 3: 21. 1905.

On Gouania polygama (Jacq.) Urban., Vicosa, June 5, 1933, II, 600.

Known in South America only from Brazil and Colombia.

Puccinia graminis Pers. Neues Mag. Bot. 1: 119. 1794.

On *Triticum aestivum* L., Vicosa, Dec. 12, 1933, 648; Bello Horizonte, Oct. 14, 1936, 1106.

Puccinia Henningsii Dietel, Hedwigia 36: 31. 1897.

On Baccharis genistelloides (Lam.) Pers. Vicosa, Dec. 30, 1933, 670.

Heterothalamus brunioides Less., Vicosa, Feb. 15, 1934, 720.

The collection on *Heterothalamus* is placed here where it fits very well. It is obviously not *P. Heterothalami* Jackson & Holway, the only rust described on the genus *Heterothalamus*, the teliospores being colorless and not thickened above.

Puccinia heterospora Berk. & Curt. Jour. Linn. Soc. 10: 356. 1869.

On Paritium tiliaceum (L.) Juss., Belo Horizonte, Jan. 27, 1934, 685.

Sida spinosa L., Corintho, Mar. 2, 1936, 1006.

Sida urens L., Vicosa, April 29, 1933, 512.

Wissadula spicata Presl., Cataquazes, Jan. 25, 1935, 876.

Paritium has not been recorded before as a host for this species, which is common on many genera of the Malvaceae.

Puccinia insueta Wint. Hedwigia 26: 27. 1887.

On Stigmaphyllon sp., Vicosa, May 2, 1931, II, 266; Feb. 18, 1934, II & III, 753; July 25, 1934, II & III, 822.

From available records this rust appears to be common in Brazil.

Puccinia Jussiaeae Speg. Anal. Soc. Ci. Argent. 12: 68. 1881. On Jussiaea leptocarpa Nutt., Vicosa, June 10, 1933, 617.

Originally described from Argentina, this rust is well known in the southern United States. This appears to be the first report from Brazil.

Puccinia Kaernbachii (P. Henn.) Arth. Bull. Torrey Club 46: 110. 1919.

On Andropogon condensatus H.B.K., Vicosa, June 3, 1933, 567. Andropogon semiberbis (Nees.) Kunth., Uberlandia, May 16, 1936, 1071.

Andropogon sp., Vicosa, Nov. 24, 1929, 30. Imperata braziliensis Trin., Vicosa, Mar. 20, 1930, 154.

Puccinia Lantanae Farl. Proc. Am. Acad. Sci. 18: 83. 1883. On Lantana trifolia L., Vicosa, Dec. 23, 1933, 666.

Puccinia lateritia Berk. & Curt. Jour. Phila. Acad. Sci. 2: 281. 1853.

On Borreria latifolia (Aubl.) Schum., Vicosa, Jan. 7, 1930, 115. Diodia prostrata Sw., Uberlandia, May 16, 1936, 1078.

Puccinia Leonotidis (P. Henn.) Arth. Mycologia 7: 245. 1915. On Leonotis nepetaefolia (L.) R. Br., Vicosa, April 21, 1933, II & III, 480.

Puccinia Levis (Sacc. & Bizz.) Magnus, Ber. Deuts. Bot. Ges. 9: 190. 1891.

On Brachiaria plantaginea (Link) Hitch. = Panicum plantaginea, Vicosa, Mar. 22, 1933, 417.

Panicum Millegrana Poir., II & III, Vicosa, Mar. 29, 1933, 429.

Panicum Sellowii Nees, Vicosa, June 3, 1933, 565.

Paspalum pilosum Lam., Vicosa, Mar. 22, 1933, 418; June 4, 1933, 588; Dec. 23, 1933, 664.

Paspalum Urvillei Steud., Vicosa, June 3, 1933, 571. Tricholaena rosea Nees, Vicosa, Dec. 3, 1929, 40.

Specimen 565 has uredospores with four equal pores and teliospores slightly smaller than normal. Specimen 571 has spores darker in color than is usual, but agrees well in all other respects.

- Puccinia liberta Kern, Mycologia 11: 142. 1919.
- On Eleocharis nodulosa (Roth) Schultes, Vicosa, April 21, 1936, 1046.
- Puccinia Malvacearum Bertero; Mont. in C. Gay, Fl. Chile 8: 43 1852.
- On Althea rosea (L.) Cav., Vicosa, Dec. 12, 1933, 649.

  Malva parviflora L., Lacutinga, Nov. 3, 1934, 858.

  ?Malva rotundifolia L., Vicosa, Mar. 5, 1932, 307.

  Malva sylvestris L., Vicosa, June 10, 1932, 351.

  Malvastrum coromandelianum (L.) Garcke Sapacahy, Nov. 3, 1934, 857.
- Puccinia medellinensis Mayor, Mém. Soc. Neuch. Sci. Nat. 5: 497. 1913.
- On Hyptis muricata Schott., Vicosa, June 22, 1935, 943. Hyptis sp., Vicosa, May 21, 1933, 547.

These specimens bear only uredinia and are referred here not without some doubt. The spores, however, appear typical, are small and thin-walled.

- Puccinia offuscata Arth. Bull. Torrey Club 47: 469. 1920. On Zornia diphylla (L.) Pers., Vicosa, Mar. 12, 1935, 882.
- Puccinia oblectaneus Jackson & Holway, Mycologia 18: 146. 1926.
- On Rynchospora aff. corymbosa (L.) Britton, Uberaha, May 15, 1936, 1075.
- Puccinia Oxalidis (Lév.) Dietel & Ellis; Dietel, Hedwigia 34: 291. 1895.
- On Ionoxalis martiana (Zull.) Small, Vicosa, May 8, 1930, 174.
- Puccinia paspalicola (P. Henn.) Arth. Man. Rusts of U. S. & Canada p. 127. 1934.
- On Panicum millegrana Poir., II, Vicosa, Mar. 11, 1933, 401.

  Paspalum conjugatum Berg., Vicosa, Dec. 12, 1933, 650.

  Paspalum mandiocanum Trin., Vicosa, May 8, 1930, 172;

  March 30, 1933, 435.

Paspalum paniculatum L., Vicosa, Dec. 4, 1929, 70.

Paspalum plicatum Michx., II, Curvello, Mar. 1, 1935, 1003, 1004; Corintho, Mar. 1, 1936, 1005.

Syntherisma digitata (Sw.), Hitch., II, Vicosa, May 20, 1933, 540.

Syntherisma sanguinalis (L.) Scop., Uberlandia, May 16, 1936, 1007.

Puccinia paulensis Rangel, Arch. Jard. Bot. Rio-de-Janeiro 2: 70. 1918.

On Capsicum frutescens L., O, I, III, Vicosa, Nov. 16, 1929, 25. Capsicum microcarpon DC., I, III, LaVras, July, 1934, 987.

This is apparently an opsis form, and agrees well with Rangel's description and drawings. We have not had any authentic specimen for comparison.

Puccinia Polygoni-amphibii Pers. Syn. Fung. 227. 1801. On *Persicaria setacea* (Baldw.) Small, Vicosa, June 10, 1933, II, 612.

Puccinia Polypogonis Speg. Anal. Mus. Nac. Buenos Aires 19: 300. 1909.

On Polypogon elongatus H.B.K., Cajury, Oct. 12, 1931, 294.

Was taken at Barbacena Minas Geraes, by Holway no. 1392.

Puccinia Porophyllui P. Henn. Hedwigia Beibl. 39: 153. 1900. On *Porophyllum ellipticum* DC., Vicosa, Feb. 26, 1930, 198.

Puccinia Pithecocteniii Paz. Hedwigia 30: 199. 1891. On Pithecoctenium cordifolium Mart., Vicosa, June 8, 1933, 608.

Puccinia Psidii Wint. Hedwigia 23: 171. 1884.

On Eugenia sp., Ana Florencia, Nov. 3, 1932, 378; Vicosa, Mar. 31, 1931, 252.

Jambos Jambos (L.) Millsp., Ponte Nova, May 3, 1930, 170. Marlierea edulis Niedenzu, Vicosa, May 30, 1932, 348. Myrcia sp., Vicosa, Oct. 23, 1931, 298.

Myrciaria cauliflora Berg., Vicosa, Dec. 8, 1929, 74; Vicosa, Oct. 22, 1936, 1114.

Myrtaceae sp. indet., Vicosa, Jan. 7, 1930, 116.

Psidium Guajava L., Sylvestre, Feb. 20, 1932, 303.

Psidium sp., Araponga, Apr. 30, 1932, 337.

On Myrciaria (Specimen 74) are abundant telia as well as uredinia. The teliospores are irregularly ellipsoid,  $18-20 \times 34-50 \,\mu$ , usually somewhat constricted; wall pale cinnamon-brown, about  $1.5 \,\mu$  thick, not or only slightly thickened above, smooth. Uredo Rochaei Putt. is the only rust known to us to have been reported on Myrciaria. While no specimen of it has been seen, it seems likely that it will be found to be identical with P. Psidii.

Puccinia Pterocauli P. Henn. Hedwigia 35: 240. 1896. On Pterocaulon alopecuroideum (Sw.) DC., II, Crasto, April 30, 1933, 518.

Pterocaulon pycnostachyum (Lam.) DC., II, Vicosa, April 21, 1936, 1048.

This specimen bears only urediniospores which agree with the brief description Sydow, Monog. Ured. 1: 138. We have had no authentic specimens for comparison.

Puccinia purpurea Cooke, Grevillea 5: 15. 1876.

On Holcus halepensis L., Vicosa, Nov. 19, 1930, 217.

Holcus Sorghum L., Vicosa, Nov. 11, 1929, 59; Mar. 1, 1934, 745.

Sorghum arundinaceum (Willd.) Stapf., Pedro Leopoldo, Jan. 27, 1934, 686.

Sorghum arundinaceum appears to be a new host.

Puccinia Rhamni (Pers.) Wettst. Verh. Zool.-Bot. Ges. Wien 35: 545. 1886.

On Avena sativa L., Vicosa, Feb. 23, 1931, 240; Nov. 9, 1931, 271; Lavras, Sept. 1933, 985.

Puccinia rotundata Dietel, Hedwigia 36: 32. 1897.

On Vernonia brasiliana (L.) Ekm., Corintho, Mar. 2, 1936, 1008. Vernonia aff. crotonoides, Vicosa, June 8, 1933, 609. Vernonia ferruginea Les., Uberlandia, May 17, 1936, 1076. Puccinia ruderaria Jackson & Holway, Mycologia 24: 153. 1932.

On Baccharis oxyodonta DC., Vicosa, Sept. 2, 1934, 835.

Known only from Brazil.

Puccinia rubigo-vera (DC.) Wint. in Rab. Krypt.-Fl. 1: 217. 1881.

On Triticum aestivum L., Bello Horizonte, July 13, 1935, 955.

Puccinia Sorghi Schw. Trans. Am. Phil. Soc. II. 4: 295. 1832. On Zea Mays L., Vicosa, Oct. 11, 1929, 50; Feb. 24, 1932, 306.

Puccinia spilanthicola Mayor, Mém. Soc. Neuch. Sci. Nat. 5: 531. 1913.

On Spilanthes acmella L., Vicosa, May 3, 1934, 783.

Spilanthes ocymifolia (Lam.) A. H. Moore, Vicosa, Dec. 20, 1933, 660.

Puccinia substriata Ellis & Barth. Erythea 5: 47. 1897.

On Chaetochloa geniculata (Lam.) Millsp. & Chase, II, Vicosa, Jan. 4, 1930, 114.

Paspalum mandiocanum Trin., Vicosa, Dec. 20, 1933, 661. Paspalum paniculatum L., Vicosa, June 6, 1933, 570. Paspalum plicatum Michx., Vicosa, Mar. 12, 1932, 313.

RAVENELIA INDIGOFERAE Tranz. Hedwigia 33: 369. 1894. On Indigofera Anil L., II & III, Vicosa, May 20, 1934, 788.

Sphenospora yurimaguasensis (P. Henn.) Jackson, Mycologia 18: 153. 1926.

On Smilax papyracea Poir., Vicosa, April 29, 1933, 513.

Tranzschelia punctata (Pers.) Arth. Résult. Sci. Congr. Bot. Vienne 340. 1906.

On Amydalus (nectarine), Vicosa, Feb. 12, 1935, 873.

Prunus domestica L., Vicosa, Feb. 1, 1930, 117.

Amydalus Persica L., Vicosa, Oct. 8, 1929, 49.

UREDO BORRERIAE (P. Henn.) Kern & Whetzel, Mycologia 18: 42. 1926.

On Borreria sp., Vicosa, May 8, 1935, 935.

## Uredo Cassiae-rugosae sp. nov.

Uredosoriis hypophyllis, numerosis, sparsis vel in maculis bruneolis aggregatis, 0.2–0.4 mm. diam. mox nudis pulverulentis obscure cinnamomeo-brunneis; paraphysibus nullis; uredosporis ellipsoideis vel obovoideis,  $19-23 \times 26-35 \,\mu$ ; tunica aurato-vel pallide cinnamomeo-brunnea,  $1-1.5 \,\mu$  cr. dense echinulata; poris 3–4 equatorialibus.

On Cassia rugosa Don., Uberlandia, May 19, 1936, 1083.

UREDO CUPHEAE P. Henn. Hedwigia 34: 99. 1895. On Cuphea sp., Uberlandia, May 16, 1936, 1073.

UREDO ERYTHROXYLONIS Graz. Bull. Soc. Myc. Fr. 7: 152. 1891. On Erythroxylon ovifolium Peyr., Ouro Preto, May 1, 1933, 522. Erythroxylon Pelleterianum St. Hel., Vicosa, June 3, 1933, 569.

UREDO HYMENAEAE Mayor, Mém. Soc. Neuch. Sci. Nat. 5: 585. 1913.

On Pettogyne discolor Vog., Herval, May 29, 1934, 785.

This is a new host for Mayor's *Uredo*, also a first report for Brazil.

UREDO MACELLA Jackson and Holway, Mycologia 18: 150. 1926. On *Juncas* sp., Vicosa, April 21, 1936, 1047.

UREDO MELINIDIS Kern, Mycologia 30: 550. 1938. On Melinis minutiflora Beauv., Vicosa, July 28, 1930, 202.

Originally described from Venezuela, where three collections have been made. This constitutes the second report of the species.

UREDO PSYCHOTRIICOLA P. Henn. Hedwigia 34: 321. 1895. On *Palicourea* sp., Vicosa, May 26, 1934, 808.

We have had no opportunity to study an authentic specimen of *Uredo psychotriicola*. Consequently this disposition of our speci-

men is not without some doubt. It is certainly not unlike *Puccinia* fallaciosa which is known only from North America. Telia are lacking, however, and the markings on the urediospores are coarser than those of *P. fallaciosa*, and agree well with Henning's description of *U. psychotriicola* which was described from Brazil.

UREDO TERMINALIAE P. Henn. Hedwigia 34: 321. 1895. On Terminalia hylobates Eichl., May 17, 1936, 1074.

While we have no authentic specimen for comparison, this collection agrees well with the description (Sydow, Monog. Ured. 4: 445. 1924). The four pores are often basal, rather than equatorial.

UREDO TRICHILIAE Arth. Mycologia 9: 90. 1917. On *Trichilia Weddellii* C.O.C., Vicosa, Mar. 24, 1933, 421.

UREDO ULEANA Dietel, Hedwigia 36: 36. 1897. On *Heteropteris coriaceae* Juss., Lagoa Santa, July 16, 1935, 959.

Uredo Uleana was described by Dietel from a specimen of E. Ule collected in Minas Geraes and said to be on some undetermined Malpighiaceae. No specimen has been available for comparison but the collection here cited agrees so well with Dietel's description that it is placed here with confidence.

# Uredo vicosiana sp. nov.

Uredosoris hypophyllis, sparsis vel paucis in maculis decoloratis dispositis, minutis, 0.2–0.5 mm. diam., pallide flavis, pulverulentis; epidermide rupta visibili; uredosporis late ellipsoideis,  $16-19 \times 19-25 \,\mu$ ; tunica subhyalina,  $1-1.5 \,\mu$  cr., minute verrucosa; poris obscuris.

On Cleome spinosa Jacq., Vicosa, Feb. 4, 1934, 689.

Other rusts on *Cleome* are *Puccinia Cleomis*, a micro form, and aecia of *Puccinia subnitens*. No previous record of a *Uredo* has been found.

Uromyces Anguriae Jackson & Holway, Mycologia 24: 101. 1932.

On? Gurania aff. pycnocephala Harms., Vicosa, Apr. 1, 1933, 440.

This species which was described from Brazil on Anguria Warmingiana differs from the several others on the family Cucurbitaceae

in having verrucose teliospores. It is supposed to be an autocious eu form, but aecia have not been described. This is the second report of the species. While there is some doubt about the host species, the rust agrees well with the type and is placed here without hesitation.

Uromyces appendiculatus (Pers.) Fries, Summa. Veg. Scand. 514. 1849.

On Phaseolus vulgaris L., II, Vicosa, Feb. 7, 1930, 103.

UROMYCES ASCLEPIADIS (Schw.) Cooke, Grevillea 5: 152. 1879. On Asclepias curassavica L., II, Vicosa, June 4, 1933, 587.

UROMYCES BIDENTICOLA (P. Henn.) Arth. Mycologia 9: 71. 1917.

On Bidens pilosa L., II, Vicosa, Jan. 7, 1934, 674; Feb. 17, 1934, 728.

Bidens rubifolius H.B.K., II & III, Vicosa, May 2, 1931, 267.

Uromyces Blainvillae Berk. Jour. Linn. Soc. 14: 92. 1873. On *Blainvillea rhomboidea* Cass., Leopoldina, July 16, 1934, 826.

Uromyces Bomareae P. Henn. Hedwigia 38: 67. 1899. On *Bomarea* sp., II & III, Vicosa, Dec. 3, 1929, 41.

UROMYCES DOLICHOSPORUS Dietel & Holway; Holway, Bot. Gaz. 31: 327. 1901.

On Tournefortia villosa Salzm., Vicosa, April 8, 1933, 449.

UROMYCES ERAGROSTIDIS Tracy, Jour. Myc. 7: 281. 1893. On *Eragrostis pilosa* (L.) Beauv., II, Vicosa, Feb. 12, 1930, 123.

UROMYCES FABAE (Pers.) DeBary, Ann. Sci. Nat. IV. 20: 80. 1863.

On Vicia Faba L., Vicosa, Nov. 18, 1929, 26.

Uromyces Hedysari-paniculati (Schw.) Farl.; Ellis, N. Am. Fungi 246. 1879.

On Desmodium supinum (Sw.) P.DC., Vicosa, May 20, 1933, 541.

This collection bears telia which are not common in other South American collections. They resemble the telia found in North America, but there may be some doubt as to whether any South American collections are properly referred to this species.

?UROMYCES IMPERFECTUS Arth. Bull. Torrey Club 47: 472. 1920.
On Bauhinia Nurandiana Pittier, Ureraba, May 15, 1936, 1077.
Bauhinia sp., II & III, Cajury, Oct. 13, 1931, 296; Vicosa, Feb. 17, 1934, 741.

Whether this is the same as *U. superfixus* Vesterg, as suggested in Venezuela list (Monog, Univ. Puerto Rico Ser. B, no. 2: 301, 1934) is still a question. Specimen 296 bears mostly telia, but a few uredospores are present. Specimen 741 bears only the uredo stage. These Uredos agree with Arthur's species and the telia which have only a pale umbo could not be called coronate.

UROMYCES LEPTODERMUS Sydow; Sydow & Butler, Ann. Myc. 4: 430. 1906.

On Panicum antidotale Retz., II & III, Vicosa, May 3, 1934, 784; II, Vicosa, Jan. 3, 1935, 862; II, Vicosa, June 22, 1935, 984.

The best collection of telia seen. This is an Asiatic grass and not a native of Brazil. Since the rust was originally described from East India this may explain the abundant development of telia which have been rarely found on collections from the Western Hemisphere.

Uromyces Medicaginis Pass. Thüm. Herb. Myc. Oecon. 156. 1874.

On Medicago sativa L., II, Bello Horizonte, Nov. 1, 1929, 185.

UROMYCES NOVISSIMUS Speg. Anal. Soc. Ci. Argent. 10: 134.

On Cayaponia aff. racemosa (Sw.) Cogn., II & III, Vicosa, Mar. 11, 1933, 402.

Whether this species is actually distinct from *U. Hellerianus* Arth., as applied to collections from Central America and the West Indies, is doubtful. More ample collections from South America would no doubt clear up this point.

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UROMYCES ORBICULARIS Dietel, in Hedwigia 36: 28. 1897. On *Meibomia* sp., I & III, Bello Horizonte, Jan. 1, 1934, 687.

The epiphyllous telia associated with hypophyllous aecia and the absence of uredinia seem to make this species quite distinct.

UROMYCES PROEMINENS (DC.) Pass. Rab. Fungi Eur. 1795. 1873.

On Chamaesyce hirta (L.) Millsp., I, II, III, Vicosa, Mar. 12, 1930, 150.

Uromyces ratus Jackson & Holway, Mycologia 24: 102. 1932. On Cayaponia pentaphylla Cogn., II, Vicosa, May 25, 1933, 550.

Agrees well with the type although no teliospores were found.

UROMYCES SCLERIAE P. Henn. Hedwigia Beibl. 38: 67. 1899. On Scleria sp., II & III, Vicosa, April 22, 1933, 487.

UROMYCES SPERMACOCES (Schw.) M. A. Curt. Cat. Pl. N. Car. 123. 1867.

On Spermacoce tenuior L., II, Vicosa, April 18, 1933, 472.

We have no previous record of this rust in South America. Our specimen bears only urediniospores and consequently is placed here with some doubt.

THE PENNSYLVANIA STATE COLLEGE, STATE COLLEGE, PENNA.

# SPECIES OF CORDYCEPS 1

E. B. MAINS

(WITH 2 FIGURES)

Recently the writer had the privilege of studying specimens of Cordyceps in the Farlow Herbarium of Harvard University, the Mycological Herbarium of the New York Botanical Garden, and the Mycological Collections of the United States Bureau of Plant Industry, and he wishes to express his appreciation to D. H. Linder, F. J. Seaver and J. A. Stevenson for the help and facilities afforded. Results of this study are included in the following account. One species, Cordyceps myrmecophila, obtained by A. H. Smith during the summer of 1939 is also discussed.

## CORDYCEPS UNILATERALIS (Tul.) Sacc.

This is a very interesting species on ants. It is fairly common in the tropics but has been rarely collected in the United States, being reported only from Michigan (as C. formicivora Schroet., 17), Maine (16) and North Carolina (9). There is also a specimen in the Herbarium of the New York Botanical Garden on the ant, Camponotus castaneus var. americanus collected by M. E. Smith at A. and M. College, Mississippi, and another in the Mycological Collections of the United States Bureau of Plant Industry, on an ant collected by L. E. Miles at Wiggins, Mississippi.

## Cordyceps monticola sp. nov.

Clavis capitatis, 2–2.5 cm. longis, stipitibus subcinereis, 1.5–2 mm. crassis, capitibus subglobosis, brunneo-cinereis,  $3\times3$ –4 mm.; peritheciis immersis, fusoideo-ovoideis, 600– $660\times200$ – $240\,\mu$ ; ascis cylindriceis 420– $510\times5$ – $6\,\mu$ ; ascosporis filiformibus, articulis ascosporarum 6– $8\times1.5\,\mu$  (FIG. 1, A & B).

In Gryllotalpa hexadactyla, Vonore, Tennessee, VI. 1935, G. L. Williams.

This specimen has several capitate clavae arising between the head and thorax of the insect and one from between the thorax

<sup>&</sup>lt;sup>1</sup> Papers from the Department of Botany and the Herbarium of the University of Michigan.

and abdomen. The stipes are light-gray and coalesce for part of their length. Two of the clavae have brownish-gray, globoid heads which are punctate with the dark brown ostioles. The type specimen is in the Mycological Collections of the United States Bureau of Plant Industry.

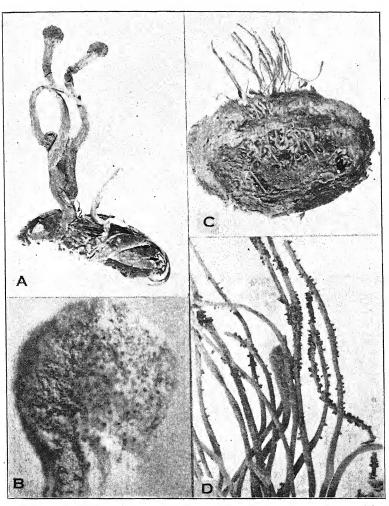


Fig. 1. A, B. Cordyceps monticola, type specimen. A, clavae arising from Gryllotalpa hexadactyla,  $\times$  2.4; B, head showing ostioles of embedded perithecia,  $\times$  12. C, D. Cordyceps crinalis, type specimen. C, clavae arising from larva in cocoon,  $\times$  1; D, clavae showing superficial scattered perithecia,  $\times$  10.

Under the name Cordyceps Gryllotalpae, Lloyd (8) has reported a collection in the Herbarium of the New York Botanical Garden. This was apparently named by Curtis but not published. Lloyd gives a photograph but no description other than that the specimens are immature. On account of the lack of description and immature condition it is not possible to determine whether this is the same as the Tennessee collection.

Lloyd also states on very insufficient evidence that *Cordyceps Gryllotalpae* and *C. joaquiens* are the same. The latter was described by Hennings (5) and the host doubtfully given as the larva of a beetle. *Cordyceps monticola* differs in a number of important respects.

Petch (15) has reported *Cordyceps amazonica* Henn. on mole cricket from Trinidad. This species has much smaller perithecia and asci than *C. monticola*.

## CORDYCEPS GRACILIS Mont. & Dur.

Among the specimens of *Cordyceps* in the Curtis Collection of the Farlow Herbarium of Harvard University is a collection with the following data: "*Sphaeria entomorrhisa* Dicks. inter folia ad larvum, Hillsboro, N. C. 1863." There is one capitate clava arising from the head of a caterpillar. The clava is 1.5 cm. long with a stalk 2 mm. thick and a globose, smooth head, 4 mm. in diameter. The caterpillar is surrounded by mycelial strands.

As has been pointed out by Lloyd (6) and others, Dickson's name has been generally misapplied to *Cordyceps gracilis*. Petch (14) has questioned the occurrence of *C. gracilis* in America and has concluded that the fungus reported as such is *C. Glaziovii* P. Henn., a similar species on beetle larvae in South America. There seems no question but that the Curtis specimen is *C. gracilis*. Both the host and the development which Petch emphasizes are those of *C. gracilis*.

# CORDYCEPS CRINALIS Ellis ex Lloyd.

In 1892, Ellis and Everhart (4) under the name *C. Sphingum*, published a detailed description and illustration of a *Cordyceps* collected at Newfield, N. J. In 1920, Lloyd (8) stated that Ellis

had named the specimen *Cordyceps crinalis* but afterwards had concluded that it was *C. Sphingum*. Lloyd decided that it was not *C. Sphingum* and that Ellis' manuscript name should apply.

The specimen in the Herbarium of the New York Botanical Garden bears the name Cordyceps crinalis Ellis & Ev. with a line drawn through the specific name and C. Sphingum written underneath. It also bears the following statement, "on larva enclosed in its cocoon attached to a decaying limb lying on the ground in the swamp, Newfield, Aug. 7, '87." The cocoon has been opened exposing the lepidopterous larva within. The clavae are now somewhat broken. They are numerous, brownish-gray, filiform, up to 4.5 cm. long, and 0.2-0.3 mm. thick (FIG. 1, C & D). The perithecia are chestnut-brown, superficial, free, scattered or crowded on the upper part of the clavae, ovoid with obtuse apices, 310- $360 \times 180-240 \mu$ . The asci are slightly fusoid,  $150-180 \times 8-9 \mu$ , narrowing to 3-4  $\mu$  above. The ascospores are filiform, somewhat overlapping in the ascus,  $1.5 \mu$  thick, obscurely multiseptate. Ellis and Everhart state that there were approximately 30 clavae which were about 5 cm. long and that a few were sparingly branched above.

This as Lloyd has indicated is a valid species. It is closely related to *Cordyceps acicularis* from which it differs in having smaller perithecia and asci and more numerous caespitose clavae. *Cordyceps acicularis* has been reported only on larvae of beetles.

## CORDYCEPS RICKII Lloyd.

Cordyceps Rickii was published by Lloyd (8) in 1920 with a brief description and several figures. Lloyd compared it with C. submilitaris from which he concluded it was distinct. Petch (14) in 1933 decided that it was synonymous with C. martialis in which species he also placed C. submilitaris. Later Petch (16) has suggested that C. Rickii might be C. Melolanthae.

The collections of this species (37238 type, 41268 and 41275) in the Lloyd Herbarium, now in the Mycological Collection of the United States Bureau of Plant Industry have been examined. Usually several clavae arise from a large white larva of a beetle. The clavae are club-shaped or irregularly furcate, 3.5–6 cm. long (Fig. 2, A). The stipes are brown, 3–5 mm. thick and often co-

alesce. The fertile portion is light brown to brownish-yellow, and is up to 2 cm. long and 5–10 mm. thick. The perithecia are entirely embedded and are ovoid, 540– $600 \times 200$ – $240 \mu$ .

Cordyceps Rickii is very distinct from both C. submilitaris and C. martialis, both of which have orange to red clavae. It does not differ greatly from C. Melolanthae. The latter tends to have somewhat thicker clavae with the fertile stroma irregularly distributed more or less in patches on the upper part of the clavae. The differences, however, are not sufficient to separate them as species and C. Rickii should be considered a synonym of C. Melolanthae.

# CORDYCEPS (TORRUBIELLA) ARACHNOPHILA Thaxter.

This name was published by Thaxter (20) in 1914 in an article concerning the genus Aschersonia. No description is given, only the statement that in some cases the perithecial stages of Aschersonia "might at first be mistaken for a common Cordyceps (Torrubiella) arachnophila which is often found on leaves with or without its imperfect or Isaria (Gibellula) condition." No description of this species has been located.

In the Farlow Herbarium, however, there is a collection (Farlow Herb. no. 6169) on a spider made by R. Thaxter, Aug. 2, 1896. at Cranberry, N. C., which is labeled Cordyceps arachnophila. This has a few perithecia associated with a Gibellula stage. There is also another collection of this species (Farlow Herb. no. 4122) under an unpublished name. This contains a number of small spiders bearing perithecia and the Gibellula stage. The spiders are covered with a white or yellowish cottony mass of mycelium, only the legs sometimes showing. The perithecia are brown and develop directly from the mycelial covering (FIG. 2, B). They are conical ovoid, 840–1200  $\times$  300–360  $\mu$ . The asci are narrowly cylindric,  $600-660 \times 5-7 \mu$  and the ascospores filiform, nearly as long as the asci and are  $1.5 \mu$  wide and multiseptate, the septa  $6-10\,\mu$  apart. The conidial stage develops on clavae which are up to 7 mm. long, 0.1-0.2 mm. thick and which enlarge at the apices up to 0.2-0.4 mm. The clavae are covered with a network of brownish, septate hyphae from which the conidiophores arise. The hyphae and conidiophores have rough walls. The conidiophores are up to  $180 \mu$  long and  $8 \mu$  wide. The terminal cell is smooth, hyaline, and slender and supports a spherical head which is  $36\text{--}42~\mu$  in diameter and consists of brownish, clavate, radiating cells from which hyaline cylindric conidia are produced. The conidia are  $4\text{--}6\times1\text{--}1.5~\mu$ . The conidial stage is apparently Gibellula aranearum.

The lack of perithecial clavae and the development of perithecia on the mycelial covering would place this species in the genus

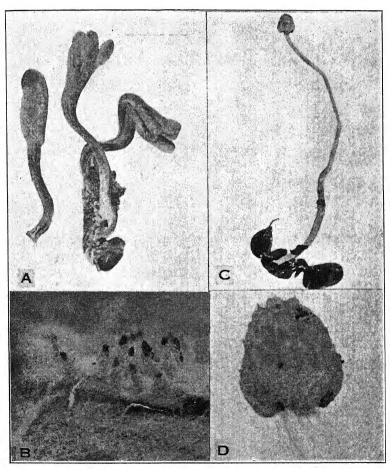


Fig. 2. A, Cordyceps Rickii, type specimen,  $\times 1$ ; B, Torrubiella Gibellulae showing perithecia,  $\times 10$ ; C, D, Cordyceps myrmecophila: C, clava arising from an ant,  $\times 2.4$ ; D, head showing obliquely embedded perithecia,  $\times 12$ .

Torrubiella. In 1932, Petch (13) announced the discovery of perithecia associated with Gibellula aranearum in collections from Ceylon and Trinidad to which he gave the name Torrubiella Gibellulae. His description of the species differs from the above in having smaller perithecia and asci. However a study of collections of Torrubiella Gibellulae in the Farlow Herbarium determined by Petch indicates that the species ranges in size up to the measurements given above. Since Thaxter's name was published without a description it must therefore be listed as a nomen nudum under Torrubiella Gibellulae Petch.

#### CORDYCEPS CUSU Pat.

In 1895 Patouillard (12) gave the name *C. Cusu* to a specimen from San Jorge, Ecuador. The host is given as the larva of a beetle and it is stated that all the clavae were sterile. The specimen in the Patouillard collection in the Farlow Herbarium of Harvard University was examined. It apparently is a sterile plant of *Cordyceps Rickii* and the name therefore should be placed in the synonymy of *Cordyceps Melolanthae*.

### Cordyceps Cockerellii Ellis.

Ellis (3) described a species as Ophionectria Cockerellii from specimens received from T. D. A. Cockerell and a short time later (2) changed the name to Cordyceps Cockerellii. Cockerell (2) stated that the hosts were the moths, Philampelus vitis and Coccytius antoeus. These specimens are in the Herbarium of the New York Botanical Garden. One specimen is covered with a meager yellowish mycelium from which a few sterile protuberances arise. The perithecia are scattered in small groups on the mycelial covering of the moth. They are superficial, free, reddish brown, ovoid,  $600-900 \times 300-400 \,\mu$ . The asci are cylindric,  $200-230 \times 5 \,\mu$  and the ascospores are filiform, nearly as long as the asci. The other specimen consists of a few short clavae bearing immature superficial perithecia.

As Lloyd (7) has pointed out *C. Cockerellii* is *C. Sphingum*, a very variable species in which sometimes clavae are not produced and the perithecia develop on the mycelial covering of the host.

CORDYCEPS ACICULARIS Rav. ex Berk.

This species was published by Berkeley (1) in 1857 and was based on a collection made by Ravenel in South Carolina. host is given as a caterpillar. Ravenel issued the species under the name C. carolinensis in his Fungi Caroliniani Exsiccati IV— 29. Specimens of this number have been examined from the collections of the Farlow Herbarium, the New York Botanical Garden, the Academy of Natural Science of Philadelphia and the Mycological Collections of the United States Bureau of Plant Industry. The hosts of all of these are larvae of a beetle of the type commonly known as wire worms. Petch (14) also reports that the specimens in the herberia of Kew and the British Museum including the specimen cited by Berkeley (Rav. 1276) are on the larvae of a beetle. The species apparently has been reported only for South Carolina and Pennsylvania (11). Specimens examined from several herbaria add collections from Connnecticut. New Hampshire and Ontario.

The following description is taken from these collections: Clavae ochraceous to grayish-brown, slender, 2–10 cm. long, 0.3–1.0 mm. thick, the apices acuminate and sterile; perithecia superficial, free, scattered or irregularly crowded on the upper portion of the clavae, ovoid,  $360\text{--}400 \times 270\text{--}300 \,\mu$ ; asci somewhat clavate,  $190\text{--}240 \times 7\text{--}10 \,\mu$ ; ascospores narrowly fusoid,  $100\text{--}220 \times 2.5\text{--}3.5 \,\mu$ , overlapping in the ascus, septa obscure, apparently not breaking into segments.

Specimens examined: South Carolina, Rav. Fungi Car. IV, 29; Lower Bartlett, N. H., Sept. 3, 1901, R. Thaxter (Farl. Herb. 4030); West Haven, Conn., 1888–1889, R. Thaxter (Farl. Herb. 6131); West Haven, Conn., Oct. 1888, R. Thaxter (Farl. Herb. 6136); Toronto, Canada, June 10, 1899, J. Fletcher (Farl. Herb.); Toronto, Canada, Oct. 1898, C. W. Nash (Myc. Coll. B. P. I.); Laurel Run, Hunt Co., Penn., Aug. 13, 1937, B. B. and L. O. Overholts (20215).

Only two of these collections (Farl. Herb. 4030 and Overholts 20215) bear perithecia. Petch (14) has also noted that many of the collections of this species are sterile. He places the species in Ophiocordyceps.

CORDYCEPS RAVENELII Berk. & Curt.

Berkeley (1) published *C. Ravenelii* in 1857 in the same article with *C. acicularis* but on the following page. Petch (14) considers this species the same as the latter and therefore places the name in synonymy with *C. acicularis*. However according to Berkeley's description and illustration, and the specimen in Ravenel's Fungi Caroliniani, *C. Ravenelii* has club-shaped clavae with obtuse or at the most acute apices which are often sterile and tends to be much darker in color, frequently chocolate-brown. Berkeley gives the hosts as larvae of *Ancylonycha* or *Rhizotrogus* beetles of the Scarabiidae. These larvae are grubs of the June beetle type. Other collections from the United States also have this type of larvae. This is apparently a valid species.

The following description is taken from the specimens listed below: Clavae chocolate-brown, club-shaped, 3–10.5 cm. long, 1.5–2.5 mm. thick below, swelling above to 2–4 mm., the apices obtuse or acute, usually covered with perithecia, sometimes sterile; perithecia superficial, free scattered or crowded on the upper portion of the clavae, dark brown, ovoid,  $300-480\times240-300~\mu$ ; asci narrowly clavate,  $180-240\times6-10~\mu$ ; ascospores cylindric,  $160-190\times2~\mu$ , somewhat overlapping in the asci, multiseptate, the cells  $22-30~\mu$  long, tardily breaking into segments.

Specimens examined; South Carolina, Ravenel Fungi Car. IV, 28; Cranberry, N. C., Aug. 1887, R. Thaxter (Farl. Herb. 4050); West Chester, Penn. (N. Y. Bot. Gar.); Ross Run, Hunt Co., Penn., May 16, 1937, L. O. Overholts (20050); Intervale, N. H., July 1, 1901, R. Thaxter (Rel. Farl. 613); South Portsmouth, Ky., John Butler (Lloyd Coll. 41279); Great Smoky Mts. Nat. Park, Aug. 18, 1938, A. H. Smith (10327).

# CORDYCEPS MYRMECOPHILA Ces.

Cordyceps myrmecophila was distributed by Rabenhorst in Koltzschii Herb. Myc. 1033 and a description published in Bot. Zeit. 4: 877. 1846. The species is described as having capitate clavae with slender stipes and ovoid heads which are sterile at the base and ridged above with the perithecia embedded, except for their apices. The color is given as ochroleuca and the host

an ant. Nylander (10) has reported the species on the ant, Formica rufa, from Finland. He describes the asci as approximately  $300 \times 6-7 \mu$ .

The species apparently has been rarely collected and information concerning it is scanty. Saccardo (18) has reported it from Italy, Finland, Britain, North America, Ceylon and Borneo. Since ichneumon flies and beetles as well as ants are listed as hosts probably other species of *Cordyceps* are included. Seaver (19) has questioned the report of the species for North America.

During the summer of 1939, A. H. Smith collected a number of specimens of a *Cordyceps* on ants in the state of Washington. From these the following description has been derived.

Clavae capitate, arising from the thorax of the hosts, slender, 1–4 cm. long, the stipes 1 mm. thick, light yellow, the heads ovoid, 2–2.5  $\times$  1.8–2 mm., ochraceous, acute, longitudinally ridged; perithecia narrowly obovoid, 660–890  $\times$  240–275  $\mu$ , embedded obliquely with the ostioles slightly projecting upward; asci cylindric, 500–630  $\times$  4–6  $\mu$ ; ascospores filiform, nearly as long as the asci, multiseptate, soon breaking into one-celled fragments, 8–10  $\times$  1.5  $\mu$  (Fig. 2, C & D).

On ants, Port Ludlow, May 30 (13865); Lake Crescent, June 2 (13955), June 3 (14006), June 7 (14157); Joyce, June 9 (14206); Storm King, Olympic Mts., June 12 (14276); Elwha River, June 23 (14575); Mt. Angeles, June 28 (14652).

Apparently these collections are *C. myrmecophila*. Previous descriptions do not mention the oblique perithecia but statements concerning the sterile base and ridged condition of the head indicate that the original specimens probably have oblique perithecia. The asci of the Washington collections are much longer than the measurement given by Nylander. However it is often difficult to obtain entire asci.

The species is closely related to *Cordyceps sphecocephala* which develops on wasps and bees. As the Tulasnes (21) have pointed out, it is a smaller species.

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# CULTURAL HISTORIES OF MELANCONIS AND PSEUDOVALSA. IV <sup>1</sup>

LEWIS E. WEHMEVER

(WITH 22 FIGURES)

The species of *Melanconis* here considered present further variations from what might be considered as our conception of a "typical" species. *M. nigrospora* represents another case in which reproduction is accomplished exclusively by ascospores, for although perithecia are formed abundantly in nature and all cultures, a conidial stage seems to be entirely lacking.

# Melanconis Juglandis var. Caryae var. nov.2

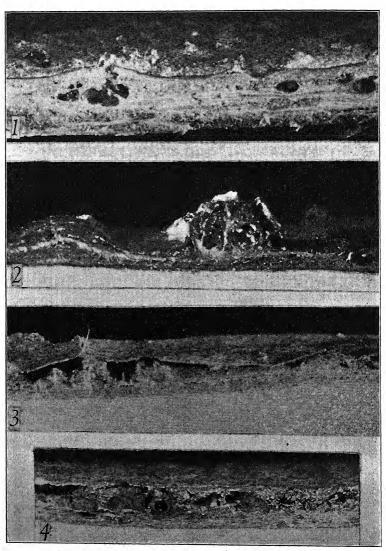
Conidia dimorpha:  $\alpha$  formae ellipsoidea vel inaequilateralia vel breviter lunata, 1-cellula, hyalina,  $10.5-14~\mu$  longa,  $5-7~\mu$  lata, in stromatibus eis Melanconii conformantia. Conidia  $\beta$  formae bacilliformis, 1-cellula, hyalina,  $2-2.5~\mu$  longa,  $0.8-1.0~\mu$  lata.

In June of 1938, a collection of a *Melanconis* on *Carya alba* was sent to the writer by J. H. Miller, from Tallahassee Shoals, Georgia. This material was at first considered a new species and perhaps should be placed as such. It shows a close relationship to *M. Juglandis* (Ellis & Ev.) Graves, however, differing chiefly in its conidial stage, a situation used for the separations of varietal rank in several other species. The perithecial stromata (Fig. 1) differ from those of *M. Juglandis* on *Juglans* chiefly in the somewhat smaller size and lighter color and their arrangement in rather definite longitudinal series. The ascospores from *Carya* (Fig. 7) measure  $17.5-23 \times 6-7$  (8.5)  $\mu$ , which places them in the narrower portion of the range of those on *Juglans* (17–23 × 6–9.5  $\mu$ ), but as only one collection is known, certainly not of specific value.

<sup>&</sup>lt;sup>1</sup> Papers from the Department of Botany of the University of Michigan, No. 710.

<sup>&</sup>lt;sup>2</sup> Melanconis Juglandis var. Caryae var. nov. Ut in forma typica sed stromatibus minoribus, circularibus, pallidis, leniter erumpentibus, confertioribus, plerumque in seriebus linearibus longitudinaliter dispersis.

Sprays of ascospores from this material were made onto nutrient agar on August 23, 1939. After forty-eight hours, the spores were found germinating by from one to three germ tubes,  $3.5-4.5~\mu$  in diameter (Fig. 8), from either the ends or the sides of the spores.



Figs. 1-4, radial sections of perithecial stromata of: 1, Melanconis Juglandis (Ellis & Ev.) Graves var. Caryae; 2, Melanconis nigrospora (Peck); 3, Melanconis Everhartii Ellis; 4, Melanconis Corni.

Single germinating ascospores transferred to oatmeal agar, grew very slowly causing a reddish brown discoloration of the agar surface and a slight superficial growth of grayish mycelium. Fruiting stromata are scarce or absent on agar cultures.

On November 2, inoculations were made onto autoclaved twigs of *Carya* sp. Growth on these twigs was slow, and after three weeks in the moist culture tubes only a superficial white cottony mycelium, about the point of inoculation, was apparent. By December 29, a number of small spherical stromata, with a white cottony surface, had appeared. Watery droplets and later yellowish to tan colored spore masses were exuded from these stromata. These first stromata were largely superficial, but others, formed later on drier portions of the twigs, were erumpent merely as grayish discs.

The ectostromata (FIG. 5) originated on the bark surface as flattened conic areas of light colored prosenchyma. The central portions of these areas grew upwards rapidly as cylindric to conic plugs which turned a gray or yellowish-brown and ruptured the overlying periderm. The conidial hymenia were initiated over the surface of shallow open cavities on the flanks or marginal flattened areas of the ectostroma, beneath the periderm. The conidia (FIG. 9) arose as apical outgrowths of simple hyaline conidiophores measuring  $17-25 \times 1.5-2 \mu$ . At maturity, these conidia were onecelled, hyaline, ellipsoid to inaequilateral or stout lunate, guttulate and  $10.5-14 \times 5-7 \mu$ . Conidia produced on agar were similar but more irregular in shape. On drier portions of the twigs, a few slender spore horns of a lighter yellow were seen and examined and found to contain a second type of conidium which was onecelled, hyaline, rod-shaped, and  $2-2.5 \times 0.8-1.0 \,\mu$ . These were sporadic in occurrence and not definitely seen attached to conidiophores, but probably represent a beta type of conidium for this species.

This occurrence of hyaline conidia in a variety of *Melanconis Juglandis*, which itself has brown conidia, corresponds to a similar situation in the variety *marginalis* of *Melanconis Alni* and the var. *carpinigera* of *M. chrysostroma*. All three of these species have hyaline ascospores, suggesting that they represent a primitive group within the genus.

# Melanconis Corni sp. nov.3

Conidia cylindrica paulum angustata vel ad mediam versus angustiora, 4-cellula, granularia, hyalina, demum 4-guttulata,  $17.5-30 \mu$  longa,  $7-8 \mu$  lata, in loculis stromatis subcompacti parvis sphaericis vel ovoideis in conidiophoris brevibus simplicibus prolata.

Scarcely visible on the surface or visible as minute pustules of papillate erumpent ostioles, 0.1–0.2 mm. in diameter, or as circular perforations, 0.2–0.3 mm. in diameter. Perithecia 400–500  $\mu$  in diameter, in small loose groups in the unaltered bark cortex; walls thick, parenchymatic. Practically no ectostroma visible. Ostioles convergent and often erumpent as a minute disc. Asci long cylindric, with a refractive ring in the apex, 150–160  $\times$  8–9  $\mu$ . Paraphyses numerous, broad, band-like, guttulate. Spores overlapping uniseriate, fusoid-ellipsoid, two-celled, brown, constricted at the septum, biguttulate, 16–25  $\times$  7–8.5  $\mu$ .

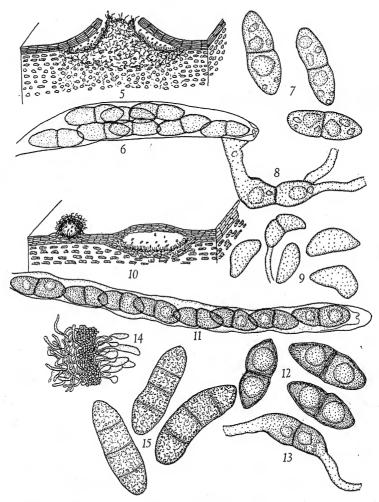
Conidia cylindric, slightly tapered or narrower in the middle, four-celled, granular, hyaline, finally 4-guttulate,  $17.5-30 \times 7-8 \mu$ , borne on short simple conidiophores in small spheric to ovoid locules within a loosely compacted stroma. Type specimen on *Cornus florida*, coll. J. H. Miller, Campus, Athens, Ga., February 20, 1939. In author's Herb.

Material of this species (FIG. 4) was sent to the writer by J. H. Miller. It was first considered to be related to Massariovalsa on account of the slight development of the ectostroma. The ascospores (FIG. 12) are smaller than those of Massariovalsa sudans (Berk. & Curt.) Sacc., however, and they are uniseriate (FIG. 11) and lack the gelatinous envelope characteristic of Massariovalsa. The conidial stage obtained in culture also indicates that its relationships must be sought elsewhere among the species of Melanconis.

Ascospores of this species germinated (FIG. 13) on nutrient agar

 $<sup>^3</sup>$  Melanconis Corni sp. nov. Vix superficialiter visibilis vel minute pustuliformis (pustulis 0.1–0.2 mm. diam. ex ostiolis papillatis erumpentibus constantibus) vel perforationes 0.2–0.3 mm. diam. circulares faciens. Perithecia 400–500  $\mu$  diam. laxe gregatim in cortice normali disposita; membranis crassis parenchymatosis. Ectostroma fere nullum. Ostiola convergentia saepe minute disciformia erumpentia. Asci longe cylindrici, apice annulo refringenti praediti, 150–160  $\mu$  longi, 8–9  $\mu$  crassi. Paraphyses numerosi late liguliformes guttulati. Spori imbricati uniseriati, fusiformes vel ellipsoidales, 2-celluli, brunnei, ad septum constricti, biguttulati, 16–25  $\mu$  longi, 7–8.5  $\mu$  crassi.

within twenty-four hours by means of germ tubes, 3–3.5  $\mu$  in diameter, put out usually first from one and then from the other end, of the spore. On nutrient agar, a black growth is formed within the medium and a slight grayish mycelium appears upon the sur-



Figs. 5-9. Melanconis Juglandis (Ellis & Ev.) Graves var. Caryac. 5, radial section of conidial ectostroma; 6, ascus; 7, ascospores; 8, germinating ascospore; 9, conidia as produced in cultures. Figs. 10-15. Melanconis Corni. 10, radial sections of superficial and intraperidermal conidial locules; 11, ascus; 12, ascospores; 13, germinating ascospore; 14, section of wall and hymenium of conidial locule; 15, conidia as formed in cultures.

face. Small grayish, hemispheric stromata soon appeared on the surface along the line of contact between the single spore colonies isolated. These stromata consisted of a loosely compacted weft of brownish hyphae, 3–3.5  $\mu$  in diameter, arising from a looser growth of upright hyphae within the agar. The hyphae were more compacted in the upper portion of the stroma, from which area a loose weft of hyaline hyphae arose. Conidia were formed at first throughout this hyaline weft. More rapid spore formation soon gave rise to a more or less open pocket filled with conidia. These conidia (Fig. 15) were cylindric oblong, tapered toward the point of attachment, or often slightly narrower in the middle, hyaline and granular at first, soon becoming four-guttulate and showing three faint septa. They measured  $17.5-26 \times 6-8 \mu$ .

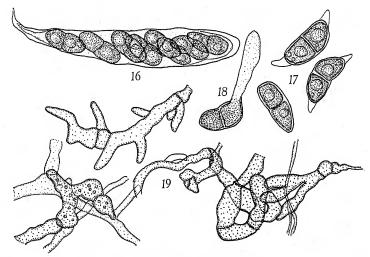
On August 8, 1939, autoclaved twigs of *Cornus florida* were inoculated from single spore cultures. Within three weeks, numerous, minute, superficial, gray, floccose stromata appeared upon these twigs, and eventually exuded yellowish masses or tendrils of conidia. These stromata (FIG. 10) on twigs arose as loosely compacted masses of hyphae, much as described for those on agar. They were formed upon the surface, within the periderm, or rarely just beneath this tissue. Conidial formation within these stromata resulted in a spheric or ovoid locule (FIG. 10) surrounded by a wall-like area of densely compacted hyphae (FIG. 14). Where exposed on the surface, these stromata were covered by a loose floccose tomentum. The conidia on twigs were four-celled, granular, hyaline,  $23-30 \times 7-8 \mu$  and very similar to those formed on agar.

This conidial stage is a type heretofore unknown in the genus *Melanconis*. *M. thelebola* has four-celled brown conidia, formed in locules, but the ascospores of that species are hyaline and appendaged and a well developed ectostroma is formed. The affinities of *M. Corni* seem to be with the Pseudoprosthecium group, such as *Pseudovalsa Ulmi* or *P. Berkeleyi*, both of which have a very slightly developed ectostroma and four-celled conidia, hyaline in the former and brown in the latter species. The difficulty in considering *M. Corni* as a two-celled progenitor of the Pseudoprosthecium group lies in the uniseriate and unappendaged condition of the ascospores which are appendaged and biseriate in Pseudoprosthecium. *M. Corni* must remain as another isolated ex-

ample of the variation of the conidial stage within the two-celled *Melanconis* group.

# Melanconis nigrospora (Peck) comb. nov.

This is an aberrant species of *Melanconis*. It was described as *Diatrype nigrospora* by Peck in 1880 (Rep. N. Y. State Mus. 33: 33), as *Melanconis Meschuttii* by Ellis in 1883 (Bull. Torrey Club 10: 117) and was placed in *Valsaria* as *V. nigrospora* by Berlese & Vogliano (Sacc. Syll. Fung., Add. 129), in 1886. The perithecia (Fig. 2) are formed in a richly developed entostroma which is usually outlined by a definite and complete, blackened, marginal zone. In this respect it resembles the genus *Valsaria*, but it differs in the broad, band-like, evanescent paraphyses and the short, hyaline, triangular appendages on the ascospores (Fig. 17). A co-



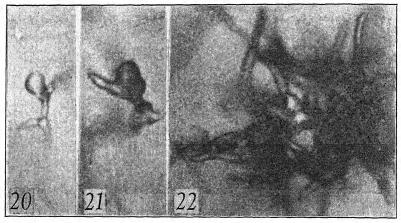
Figs. 16–19. *Melanconis nigrospora* (Peck). 16, ascus; 17, ascospores; 18, germinating ascospore; 19, various hyphal proliferations representing early stages in the formation of perithecial primordia.

nidial connection would be most desirable here, to aid in determining its relationships, but so far none has been obtained.

Isolations of single ascospores were made from twigs of Betula alba collected in Colchester Co., Nova Scotia, in 1935, and from twigs of Betula sp. collected near Howell, Michigan, in 1938. The

ascospores germinated (FIG. 18) within twenty-four hours, in both cases, by pushing out a single, short, somewhat clavate germ tube,  $3-3.5 \mu$  in diameter.

Growth on agar was slow, forming a powdery white surface growth at first, which later turned brown-black on the agar surface and eventually produced scattered, superficial, confluent, grayish stromata, 1–2 mm. in diameter, which contained numerous peri-



Figs. 20, 21, earliest stages in the formation of perithecial primordia; 22, later stage of perithecial primordium, showing proliferation to form hyphal knot.

thecial primordia, most of which remained sterile, although they were often seen with a few mature ascospores. On sterilized twigs of *Betula alba*, similar stromata were formed but in greater abundance. No conidial stage was seen in the hundreds of stromata which have been sectioned.

The origin of the perithecium can be followed in the granular marginal growth on nutrient agar but due to the fact that the majority of the perithecia fail to develop normally but form sterile, parenchymatic sclerotic bodies, instead, the details of perithecial development were not followed.

Contrary to our ideas of the origin of the sphaeriaceous perithecium as a definite structure, usually forming a coiled or "Woronin" hypha, these perithecia develop as a vegetative stromatic knot of hyphae. At the point of origin of a perithecium, several

cells of a hypha (FIGS. 20, 21) become irregularly enlarged and put out short stubby branches. This swelling and branching of the hyphae (FIG. 19) continues to form an intertwined knot which soon becomes a spherical mass of tissue (FIG. 22). These primordia arise in large numbers in more or less localized areas. The intermediate hyphae, between the primordia, also enlarge, become darkened in color and form a common stroma in which the perithecia are imbedded. As the perithecium develops, there appears a central "core" tissue of smaller dark staining, concentrically arranged, hyaline hyphae which are surrounded by several layers of dark brown parenchymatous wall tissue. In normal development, this central core gives rise to the ascogenous system within the wall, but under the conditions of agar cultures, most of the perithecial "cores" soon lose their active growth and become transformed into a large-celled pseudoparenchyma similar to that of the wall tissue.

Our knowledge of perithecial origin and development is limited to a comparatively few cases in isolated groups and the prevalent ideas of development often referred to as sphaeriaceous, pseudosphaeriaceous, and dothideaceous will undoubtedly need much revision, and many intermediate series will emerge as our information increases. This species is merely one example of a type which has been generally accepted as sphaeriaceous, from its mature structure, but which shows a type of perithecial origin of a more pseudosphaeriaceous type.

# Melanconis Everhartii Ellis.

This species (Fig. 3) has been isolated from five different collections on twigs of *Acer*. Two of these isolations were lost on account of the slow growth of the germinating ascospores and contaminations on the plates. Three were grown in agar cultures and two isolations were transferred to autoclaved twigs of *Acer Saccharum*. In no case were any indications of conidia or conidial stromata seen.

The ascospores germinate within twenty-four to forty-eight hours, by one, or occasionally two, germ tubes, 5–7  $\mu$  in diameter. On oatmeal agar a superficial, white to gray, cobwebby mycelial growth is formed and the surface layers of the agar are blackened.

Scattered, pulvinate, grayish stromata are occasionally formed on agar, but all such stromata examined have been sterile.

On twigs of *Acer*, small erumpent, grayish, ectostromatic discs, 0.5 mm. in diameter are formed. Sections of these show that a small ectostroma, composed of hyaline to brown, rather large-celled parenchyma is formed on the bark surface beneath the periderm. In the base of these stromata, or in a swollen entostromatic area beneath them, perithecial initials, composed of coiled spherical knots of hyphae, are usually found but no conidial stage has ever been seen.

It is unfortunate that no conidial stage could be obtained for this species. Its light-colored ectostromata and large, hyaline, appendaged ascospores suggest that this species may be related to *Melanconis thelebola*, which has four-celled, brown conidia. On the other hand, it might be related to such species, with appendaged ascospores, as *M. Alni*, which have a *Melanconium* imperfect stage. Without any conidial stage, the position of *M. Everhartii* must remain in doubt.

#### SUMMARY

A new variety of *Melanconis Juglandis* (Ellis & Ev.) Graves, on *Carya*, was found to produce hyaline conidia in *Melanconium*-like pustules.

A new species, *Melanconis Corni*, described from *Cornus florida*, produced four-celled hyaline conidia in locules within a loosely compacted stroma.

Melanconia nigrospora (Peck) and M. Everhartii Ellis failed to produce any conidial stage. M. nigrospora produced perithecia freely in culture. These perithecia arose from swollen, branching hyphae in a manner not usually associated with the Sphaeriales.

# A LEAFSPOT FUNGUS ON NYSSA

## FREDERICK A. WOLF

During August and September the two species of tupelo, Nyssa sylvatica Marsh and N. biflora Walt., occurring within the Duke Forest, may be found to be severely affected with a leafspot disease. The pathogen associated with this disease is one of the pycnidial Fungi Imperfecti known as Phyllosticta Nyssae Cooke. Studies of its morphology, however, have shown that P. Nyssae is not a pycnidial (conidial) stage but a spermogonial (spermatial) stage. Studies of its developmental cycle, furthermore, have shown that this spermogonial stage is genetically connected with a perithecial (ascigerous) stage that grows on decaying leaves and reaches maturity during spring of the following year. The present report, therefore, embodies the results of these studies and contributes to a better understanding of the structure and identity of this pathogen on tupelo.

#### APPEARANCE OF TUPELO LEAFSPOT AND ITS DISTRIBUTION

The incidence of this disease does not appear to be correlated with age of the trees although the foliage of small trees is commonly most severely involved. The reason for this appears to be related to the proximity of the leaves of small trees to inoculum contained in decaying leaves on the ground. The presence of scattered, irregular, purplish blotches upon the upper leaf surface constitutes the first evidence of infection. No discoloration of the lower leaf surface is apparent at this time. As the disease progresses the blotches enlarge and may become irregular areas one to three centimeters across. It is not unusual for the entire upper leaf surface to become involved. Meanwhile the lower surface of the lesions becomes dark-brown, and is thickly beset with punctiform dark, fungous structures. As these structures rupture the leaf surface it becomes somewhat cinereous. In case the lesions remain discrete, the intervening leaf areas acquire the purplish

scarlet coloration, characteristic of tupelo leaves in autumn. Premature defoliation follows. After the leaves have fallen the diseased portions become purplish-black above and dark-brown below, and the fungous structures continue to develop and to increase in number to the extent that they may rather uniformly and densely occupy the entire lower leaf surface.

Examination of exsiccati<sup>1</sup> in the Farlow Herbarium, the herbarium of the New York Botanical Garden, and the herbarium of the Division of Mycology and Disease Survey of the U. S. Department of Agriculture show that this fungus has been collected in Alabama, Florida, Georgia, South Carolina, North Carolina, Virginia, West Virginia, and Maryland. Apparently it is confined to the Southeastern United States and is not coextensive in range with that of the several species of *Nyssa*.

# IDENTITY OF THE PATHOGEN

Microscopic examination of the minute fungous structures protruding from the lower surface of the lesions shows them to be globular, to occur singly, and to be of two kinds. One kind may be identified as the fructifications of *Phyllosticta Nyssae* (2). In fact, the pathogen under consideration herein has been compared with the type of *P. Nyssae*, no. 798, collected at Darien, Georgia, by H. W. Ravenel and has been found to be specifically identical with the type. The so-called pycnidia, however, prove to be spermogonia. The interior of mature spermogonia becomes filled with rod-shaped spermatia  $3.0-3.5 \times 1.0-1.5 \mu$ . The spermatia are embedded in a gelatinous matrix that exudes in droplets or films when moisture conditions are favorable.

The other kind of fungous structures are the perithecial primordia. They are largely constituted of deeply-staining fungous parenchyma. Within each primordium there is a segmented carpogone whose trichogynal portion extends to the exterior.

Both the spermogonia and the primordia of perithecia can be

<sup>1</sup> The writer examined the collections in the herbarium of the New York Botanical Garden. These examinations were facilitated by the courtesies of Dr. F. J. Seaver. Reports on collections in the Farlow Herbarium and in the U. S. Department of Agriculture were made by Dr. D. H. Linder and Dr. W. W. Diehl, respectively. The writer is obligated to each of these mycologists and herewith extends his thanks to them.

found throughout August, September, and well into October. Toward the end of this period the spermogonia are exhausted, and little except the membranaceous spermogonial wall remains, whereas the perithecial initials appear as stromata. By late March or early April of the following spring these stromata will have become transformed into mature perithecia 60–85  $\mu$  in diameter. They are globular except for the possession of a short ostiolar papilla that projects slightly above the leaf surface. The perithecial wall is membranaceous, being constituted of thick-walled brown cells. The asci adhere in a fascicle, a characteristic that may best be detected when perithecia are crushed in water and examined under the microscope. Paraphyses are lacking. Mature asci are cylindrical-clavate, 25–30  $\times$  6–7  $\mu$ , and the ascospores tend to be biseriately arranged. The ascospores are hyaline, 1-septate, the upper cell being the broader. Ascospores, if measured a few minutes after expulsion, are  $8-10 \times 3.5-4.5 \mu$ .

As indicated by the above mentioned characteristics of the ascigerous stage, this fungus manifestly belongs in the genus Mycosphaerella (Sphaerella). A search among previously described species of this genus revealed that in 1878 Sphaerella nyssaecola was described by Cooke (1) from specimens collected on Nyssa multiflora, in South Carolina, by H. W. Ravenel. Cooke's description (1) of S. nyssaecola is as follows: "Hypophylla. Peritheciis numerossisimis, semiimmersis, brunneis, punctiformibus. Ascis clavatis, Sporidiis minutis (immaturis). Ascis .02 -+ .025 mm." This description is manifestly very inadequate and it appeared desirable to make comparison with the type specimens, Ravenel's Fungi Americani, no. 96. As a result of this comparison it was found that there is perfect agreement between the fungus under consideration, on Nyssa, and the type material of S. nyssaecola. In the light of the present observations it appears necessary to emend the description of this organism, and it is, therefore, briefly characterized as follows:

# Mycosphaerella nyssaecola (Cooke) comb. nov.

Syn. Sphaerella nyssaecola Cooke, Hedwigia 17: 40. 1878.

Sicc. Rav. Fungi Am. no. 96.

Phyllosticta Nyssae Cooke, Grevillea 12: 26. 1883.

Sicc. Rav. Fungi Am. no. 798; Ellis N. Am. Fungi no. 1168.

Perithecia hypophylla, numerosissima punctiformia, semiimmersa, brunnea, sphaerica,  $60-85~\mu$  diam.; asci cylindracei-clavati, aparaphysati, octospori,  $25-30~\times~6-7~\mu$ ; sporae vulgo distichae interdum inordinatae; inaequaliter 1-septatae, loculo superiore crassiore, constrictae, hyalinae,  $8-10~\times~3.5-4.5~\mu$ . Hab. in foliis dejectis Nyssae sylvaticae, N. biflorae, N. aquaticae, et N. ogcche.

Statum spermogonicum Phyllosticta nyssae sistit. Spermogoniis aestivo vel autumno in foliis adhuc vivis efformantis, hypophyllis. Maculis irregularibus, magnis, infra palladis, superiore purpureis. Spermogoniis punctiformibus, suberumpentibus, atris; spermatiis copiosis, bacilliformibus, 3–3.5  $\times$  1.0–1.5  $\mu$ .

Specimens from the writer's collections have been deposited in each of the herbaria previously mentioned, where they are available to mycologists.

## DISCUSSION

In the case of a few species of Mycosphaerella only, is it known at present that they lack conidia. The writer (4) recently called attention to one such fungus, Mycosphaerella fraxinicola (Schw.) House. The so-called conidial stage of this organism, Phyllosticta viridis Ellis & Kellerm., was found to be, in reality, a spermogonial stage. The developmental cycle of M. fraxinicola hence is entirely similar to that of the fungus under consideration in the present report. Many other at present detached species of conidial fungi, especially among those included in the form genus Phyllosticta, in the artificial group Bacillostictae (3) undoubtedly will be found to be spermogonial stages. The spores of most of them will probably be found incapable of functioning except as spermatia, although it is conceivable that some might function either as conidia or as spermatia. Among the reasons upon which this opinion is based is the observation that in certain species of fungi encountered, both conidia and spermatia may have the same origin and may be borne simultaneously within the same fructification.

It is well known that the genus *Mycosphaerella*, as delimited at present, contains approximately 1000 diverse species. Studies of life histories of representative species should provide a basis for cleavage of this large group into groups of naturally related species. The opinion may be ventured that none will be of greater phylogenetic interest than the group lacking conidia.

#### SUMMARY

The pathogen associated with a leafspot disease of several species of *Nyssa* has been commonly identified as *Phyllosticta Nyssae* Cooke. This organism appears to be limited in its distribution to the southeastern United States.

Lesions are evident during late summer when punctiform fructifications of the fungus are formed on the lower leaf surface. These fructifications, occurring singly, consist of interspersed spermogonia and perithecial primordia.

The spermogonial stage is identical with *Phyllosticta Nyssae*. By the following spring, the perithecial primordia will have become transformed into mature perithecia of *Mycosphaerella nyssaecola* (Cooke). Evidence of the presence of conidia in the developmental cycle of *M. nyssaecola* is lacking.

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# SOME FUNGI FROM GREECE

Const. J. Alexopoulos

(WITH 43 FIGURES)

There are comparatively few scientific publications which deal with the Greek mycoflora. Though extensive collections of Spermatophytes were made in Greece during the previous century and the beginnings of the present one, nothing seems to have been published in the way of descriptive mycology from that country before Politis (6) published his "Sulla Flora Micologica della Grecia" in 1911. Following this article, Politis has published a series of papers listing and describing fungi collected in different parts of Greece (2, 3, 4, 5, 7, 8).

In 1931, the Benaki Phytopathological Institute was established at Kephissia, near Athens, and Dr. J. A. Sarejanni, the plant pathologist at the institute, has since published two "Lists of Diseases" of native and cultivated plants of Greece. These are actually lists of pathogenic organisms occurring on different hosts. Early in 1939, Mr. C. Diapoulis (1) published a list of higher Basidiomycetes which he collected at Pelion.

In so far as could be determined, other publications dealing with Greek fungi are either phytopathological in nature, or deal with fungi causing human diseases. The fungi which cause diseases of economic plants in Greece are fairly well known, though many of them have not been systematically studied under conditions prevalent in that country. They have frequently been described in phytopathological literature and are often mentioned in popular agricultural pamphlets addressed to the farmers.

The present paper deals with a number of parasitic fungi collected by the writer in Greece from October 1938 to April 1939 while he was associated with the Institut de Chimie et d'Agriculture "Nicolaos Canellopoulos" at Piraeus. A few specimens are included which were sent to the writer's laboratory for identification and a few more which were collected in May 1937 by Palm and Alexopoulou.

Since illustrations of fungi collected in Greece are scarce in my-cological literature, it was deemed advisable to illustrate many of the species herein reported even though some are by no means rare. Drawings, for the most part, were made with the aid of a camera lucida and the oil immersion objective. Spore measurements are recorded for most species and are in some cases compared with those given in the literature from other localities outside of Greece to bring out any ecological variations which were observed.

The specimens are deposited in the Mycological Herbarium of the Institut de Chimie et d'Agriculture "Nicolaos Canellopoulos" at Piraeus, Greece, and the numbers given here are those of the Institut. Citation in Saccardo's Sylloge Fungorum is given for each specimen and in the case of those previously reported from Greece, this is followed by the author and date of the Greek report. The Figure number following the bibliographical citations refers to the illustration in the present paper.

The writer wishes to thank Dr. K. Nevros, Director of the Institut de Chimie et d'Agriculture "Nicolaos Canellopoulos," for the excellent laboratory facilities placed at his disposal for this and other studies; the administrative authorities of Kent State University for extending to him a year's leave of absence for work in Greece; Dr. Jean C. Politis, Professor of Botany at the University of Athens, for identifying some of the host plants and for the use of the botanical library of the university; Mr. Foufas of the Department of Botany, University of Athens, and Mr. C. Diapoulis of the Hellenic Ministry of Agriculture for their assistance in various ways; Mr. V. Spanopoulos of the Institut de Chimie et d'Agriculture for his assistance in the preparation of the manuscript, and all others who in any way assisted. The writer is especially grateful to his sister Miss Theodora J. Alexopoulou for the preparation of the drawings.

#### ACTINOM YCETACEAE

1. Actinomyces scabies (Thaxt.) Güssow, Bergey, Man. Det. Bact. 4th Ed., p. 507; Sarejanni, 1935.

Specimens of diseased potato tubers collected by Mr. J. Pavlakos at Kakourion, Mantineia, Nov. 16, 1938, and brought to the writer for identification of the causal organism. The organism is very

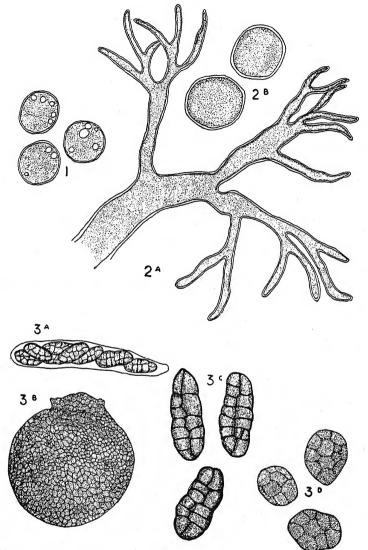


FIG. 1, Albugo candida, conidia (×750); 2, Peronospora parasitica, A, conidiophore (×750), B, conidia (×750); 3, Pleospora herbarum f. citrorum, A, ascus (×330), B, perithecium (×135), C, ascospores (×750), D, conidia from culture (×750).

common and causes considerable damage in all potato growing sections of Greece (No. 42).

#### ALBUGINACEAE

2. Albugo candida (Pers.) Roussel. Sacc. Syll. Fung. 7: 234; Sarejanni, 1935; Cystopus candidus, Politis, 1911. (fig. 1.)

A common fungus on various crucifers. Collected on Capsella Bursa-pastoris L. at Argos, Argolis, Zervos farm, on March 15, 1939. The conidia measure  $15-21 \mu$  in diameter (No. 57).

### PERONOSPORACEAE

3. Peronospora parasitica (Pers.) DeBary, Sacc. Syll. Fung. 7: 249; Politis, 1935; Sarejanni, 1935. (Figs. 2A, 2B.)

Collected on Capsella Bursa-pastoris L. at Argos, Argolis, Zervos farm, on March 15, 1939. Conidia measure  $18-29.2 \times 15.5-26.5 \mu$  (No. 56).

### HYPODERMATACEAE

4. LOPHODERMIUM PINASTRI (Schrad.) Chev. Sacc. Syll. Fung. 2:794. (FIGS. 4A, 4B.)

The few infected dry leaves of *Pinus halepensis* Mill. in this specimen were collected on Oct. 30, 1938, at Rema Loverthou, near Kephissia, Attica (*No. 31*). The asci measure 96–114.5  $\times$  11.5–12.5  $\mu$  and the ascospores, 78–86  $\times$  1.5  $\mu$ . Stevens (Fungi which cause plant disease, p. 162) records 90–120  $\mu$  for the length of the ascospores of this species. The fungus has not been previously reported from Greece.

#### MOLLISIACEAE

5. Pseudopeziza Medicaginis (Lib.) Sacc. Syll. Fung. 8: 724. (fig. 5.)

A collection from Vouliagmeni, Attica, made in May 1937 by Palm and Alexopoulou. The fungus is on diseased leaves of *Lotus corniculatus* L. and apothecia are abundant on the upper surface of the leaf, a few also being found on the lower surface. In the specimen (*No.* 47) the asci measure 80–91  $\times$  8.5–10.5  $\mu$  and the ascospores, 8–13  $\times$  3.5–4.5  $\mu$ .

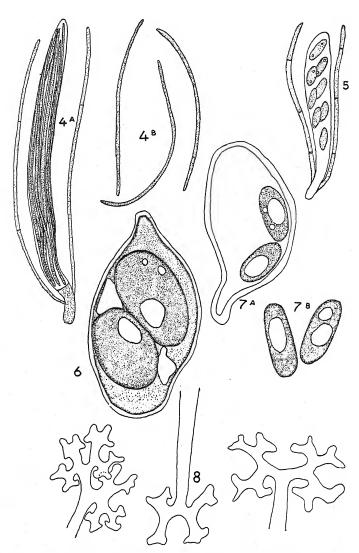


Fig. 4, Lophodermium Pinastri, A, asci with ascospores and paraphyses, B, ascospores; 5, Pseudopeziza Medicaginis, ascus with ascospores and paraphyses; 6, Phyllactinia corylea, ascus with ascospores; 7, Erysiphe Polygoni, A, ascus, B, ascospores; 8, Microsphaera Alni var. extensa, appendage tips. All × 750.

Microtome sections revealed the presence of pycnidia embedded in the leaf tissue, scattered among the apothecia. These pycnidia contain minute, bacillary pycnidiospores reminiscent of spermatia. Stevens (Ibid, p. 148) mentions that a *Phyllosticta* is thought to be the conidial stage of *Pseudopezisa Medicaginis*.

This seems to be the first report of this fungus from Greece. The same fungus was collected by the writer at Mycenae, Argolis, on *Trifolium procumbens* var. *minus*, on March 14, 1939 (No. 82).

#### ERYSIPHACEAE

ERYSIPHE POLYGONI D.C. Salm. Monogr. Erysiph. p. 174;
 Politis, 1935; Sarejanni, 1935; E. communis Sacc. Syll. Fung.
 1: 18. (FIGS. 7A, 7B.)

Collected on *Polygonum lapathifolium* L. at Florina in Macedonia (No. 6), Sept. 30, 1938, and on *Polygonum aviculare* L. at Bafi, Attica (No. 20), Oct. 25, 1938. Most of the perithecia on the Macedonian specimen were immature at the time of collection. The dimensions of the fungus taken from *P. aviculare* fall well within the limits given by Salmon. They are: Perithecia, 163–186  $\mu$ ; asci, 61–70  $\times$  41–44  $\mu$ ; ascospores, 23.5–28.5  $\times$  10.5–11.5  $\mu$ . There are from 3 to 8 asci in each perithecium, each ascus usually containing 3 or 4 spores, but the number of spores varying from 2 (FIG. 7A) to 5.

7. Microsphaera Alni (Wallr.) Salm. Monogr. Erysiph. p. 129. (fig. 8.)

This specimen (No. 12) collected at Kato Kleinai, Florina, on Sept. 20, 1938, consists of several leaves of Quercus lanuginosa Thuill., heavily infected with mycelium on which perithecia are very abundant. Oidium alphitoides G. & M., which may be the imperfect stage of this fungus, has been reported by Sarejanni (9) on Quercus coccifera L. from Greece, but the perithecial stage does not seem to have been reported in the literature from that country. The perithecia from the specimen on hand measure  $114-145 \mu$ ; the asci,  $48-65 \mu$ , and the ascospores,  $20-26 \times 13-13.5 \mu$ .

8. Phyllactinia corylea (Pers.) Karst. Salm. Monogr. Erysiph. p. 224; *P. suffulta* (Reb.) Sacc. Syll. Fung. 1: 5; Politis, 1935. (Fig. 6.)

Collected at Xylocastron, Corinthia, on March 20, 1939, on bark of *Pyrus communis* L. (*No. 64*). *P. suffulta* which Salmon considers synonymous with *P. corylea* has been reported from Attica on *Lonicera caprifolium* L. by Politis (4). Measurements from the specimen on hand are: Perithecia, 182–197.5  $\mu$ ; asci, 67–75.5  $\times$  30–39  $\mu$ ; ascospores, 36–39  $\times$  18–22.5  $\mu$ . These figures agree with those given by Salmon in his description of this species.

### PLEOSPORACEAE

9. Pleospora Herbarum (Pers.) Rabh. f. citrorum Sacc. Syll. Fung. 2: 247. (Figs. 3A, 3B, 3C, 3D.)

Specimens of diseased lemon twigs, collected at Gargalianoi, Trifyllia, were brought to the writer's laboratory for diagnosis by Mr. P. Papademetriou in November 1938. Among other fungi, Pleospora herbarum f. citrorum was found on the dried tips which had turned a characteristic grayish-white color. The perithecia of the fungus had been abundantly formed and many of them contained mature asci and ascospores. The perithecia averaged 260  $\mu$  in diameter. Asci measured 91–127.5  $\times$  24–30  $\mu$ ; ascospores, 23.5–46  $\times$  9–18  $\mu$ . These figures compare well with those given in Saccardo's description.

The fungus was taken in culture, and perithecia with asci and spores were obtained in certain media. In addition to the perithecia and much before they were developed, the fungus produced an abundance of the *Macrosporium* type conidia (Fig. 3D) which measured  $15.5-23.5 \times 13-15.5 \mu$  (No. 40).

### COLEOSPORIACEAE

 Coleosporium Inulae (Kunze) Ed. Fisch. Sacc. Syll. Fung. 21: 721; Politis, 1935.

The uredospores of this fungus were collected by Palm and Alexopoulou on leaves of *Inula attica* L. in May 1937, at Vouliagmeni Attica (*No. 49*) and by the writer on the same host on

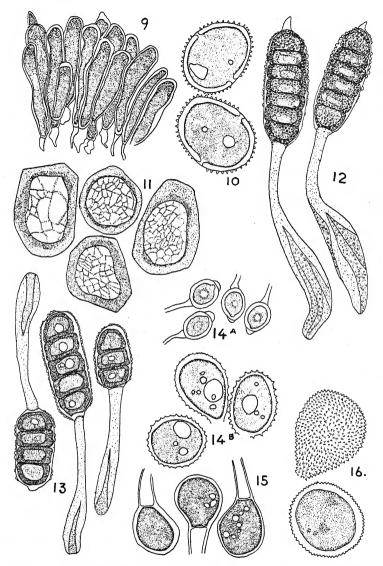


Fig. 9, Colcosporium Tussilaginis, teleutospores (× 330); 10, Uromyces Fabae, uredospores (× 750); 11, Gymnosporangium Sabinae, aeciospores (× 750); 12, Phragmidium subcorticium, teleutospores (× 750); 13, Phragmidium violaceum, teleutospores (× 750); 14, Uromyces appendiculatus, A, teleutospores (× 330); B, uredospores (× 750); 15, Uromyces Scillarum, teleutospores (× 750); 16, Uromyces Limonii, uredospores (× 750).

Nov. 5, 1938, at Daphni, Attica (No. 38). They were found to measure  $20.5\text{--}35 \times 16\text{--}23.5~\mu$  being somewhat larger than recorded by Saccardo. The teleutospores were found on leaves of *Inula viscosa* (L) Ait. at Rema Loverthou, near Kephissia, Attica, on Oct. 30, 1938 (No. 28). The teleutospores measure  $50\text{--}96 \times 22\text{--}28.5~\mu$  as compared to  $100 \times 18\text{--}24~\mu$  given by Saccardo.

11. Coleosporium Tussilaginis Tul., Grove, British Rust Fungi, p. 322; Politis, 1938. (Fig. 9.)

Though this fungus is rather common on leaves of Tussilago far-fara L., it has only recently been reported from Greece. The specimens in the present collection were taken at Bafi, Attica, on Oct. 25, 1938 (No. 22), and at Rema Loverthou, near Kephissia, Attica, five days later (No. 29). The teleutospores are up to 130  $\mu$  in length and 19–34  $\mu$  in breadth.

### MELAMPSORACEAE

12. Melampsora Euphorbiae Cast. Grove, British Rust Fungi, p. 353; *M. Helioscopiae* Wint. Sacc. Syll. Fung. 7: 586; Politis, 1911; Sarejanni, 1935.

The uredo stage was collected on March 19, 1939, at Pyrgos, Eleia, on the grounds of the A. S. O. Currant Institute, on Euphorbia helioscopia L. (No. 62). The uredospores measure 15.5–23.5  $\times$  14–18  $\mu$ , being somewhat larger in diameter than those reported by Grove. The hyaline paraphyses scattered among the uredospores measure 13–18.5  $\mu$  diam. A scant collection of teleutospore material was made in May 1937 by Palm and Alexopoulou at Vouliagmeni, Attica, on an undetermined species of Euphorbia (No. 48). The teleutospores measure 41.5–62.5  $\times$  11–14.5  $\mu$ , closely approximating in size those reported by Grove as 50–60  $\times$  10–14  $\mu$ .

#### PUCCINIACEAE

13. Phragmidium subcorticium (Schr.) Wint. Sacc. Syll. Fung. 7: 746; Politis, 1935. (fig. 12.)

A collection of leaves of cultivated Rosa taken in the Lakon garden at Kephissia, Attica, on Oct. 30, 1938 (No. 32). Measure-

ments are as follows: Uredospores,  $24-31 \times 18-22 \,\mu$ ; teleutospores,  $63-95 \times 30-36 \,\mu$ . These compare well with those given by Grove (British Rust Fungi p. 293) for *Phragmidium disci-florum* James of which he considers *P. subcorticium* a synonym.

14. Phragmidium violaceum (Schultz.) Wint. Grove, British Rust Fungi, p. 295; Sacc. Syll. Fung. 7: 744; Politis, 1935. (Fig. 13.)

Teleutospores were abundant on leaves of *Rubus ulmifolius* Schott. collected at Florina on Sept. 30, 1938 (*No. 11*), and at Bafi, Attica, on Oct. 25, 1938 (*No. 23*). They measure 41.5–116.5  $\times$  34–44  $\mu$ . Politis reports this fungus from Attica on *Rubus fructicosus*.

 GYMNOSPORANGIUM SABINAE (Dicks.) Wint. Grove, British Rust Fungi, p. 308; Sacc. Syll. Fung. 7: 739; Politis, 1935; Roestelia cancellata Reb., Sarejanni, 1935. (Fig. 11.)

A very common fungus causing considerable damage to pear trees in all parts of Greece. The *Roestelia* stage, which has been reported from Greece by Sarejanni, and others was collected on leaves of *Pyrus communis* L. at Thessaloniki, in the University Experimental Orchards on Sept. 27, 1938 (No. 5), and again at Florina in the orchards of the Florina Agricultural School, three days later (No. 8). Aeciospores from the Florina specimen measure  $26-38 \times 18-27.5 \,\mu$ .

16. Uromyces appendiculatus (Pers.) Link., Sacc. Syll. Fung.7: 535; Sarejanni, 1935; Politis, 1938. (FIGS. 14A, 14B.)

This fungus is found wherever beans are grown in Greece. Both uredo and telial stages were found when these specimens were collected, the teliosori being much more abundant. The first collection was made on Sept. 30, 1938, in the gardens of the Florina Agricultural School in Florina (No. 9), and the second on Oct. 25, 1938, at Bafi, Attica (No. 24). Measurements: Uredospores,  $21.5-31.5 \times 17-22$ ; teleutospores,  $28-35 \times 21-26 \mu$ . On leaves of *Phaseolus vulgaris* L.

17. UROMYCES FABAE (Pers.) DeBary, Grove, British Rust Fungi, p. 97; Sacc. Syll. Fung. 7: 531; Politis, 1911; Sarejanni, 1935. (Fig. 10.)

Very common in all parts of Greece. Specimens were collected at Salamis by Mr. P. Papademetriou, on Feb. 13, 1939 (No. 83), and by the writer at Thouria, Kalamai, March 17, 1939 (No. 59), and at Katerini, Macedonia, June 6, 1939 (No. 84). The last of these collections consisted of both uredo and telial stages. Spore measurements are: Uredospores,  $23.5-32.5 \times 18-26 \,\mu$ ; teleutospores,  $31-43 \times 20-25.5 \,\mu$ .

18. UROMYCES JUNCI (Desm.) Tul. Grove, British Rust Fungi, p. 123; Sacc. Syll. 7: 541. (FIG. 18.)

A scant collection of teleutospores from Kephissia, Attica, taken at Rema Loverthou, on *Juncus* sp., on Oct. 30, 1938 (*No. 30*). Teleutospores measure  $23.5–37 \times 15.5–21 \,\mu$ . This is the first report of this fungus from Greece.

19. UROMYCES LIMONII (D.C.) Lev. Grove, British Rust Fungi, p. 88; Sacc. Syll. Fung. 7: 532. (Fig. 16.)

A collection of uredospores on Limonium sinuatum Mill. taken by Palm and Alexopoulou at Vouliagmeni, Attica, in May 1937 (No. 50). Uredospores measure 26–26.5  $\times$  25.5–30  $\mu$ . This is the first report of this fungus from Greece.

 UROMYCES SCILLARUM (Grev.) Wint. Grove, British Rust Fungi, p. 120; Sacc. Syll. Fung. 7: 567; Politis, 1935. (Fig. 15.)

A scant collection taken at Mycenae, Argolis, on March 14, 1939, on leaves of *Muscari botryoides* Mill. (*No. 54*). Teleutospores measure  $18-28.5 \times 15.5-20 \,\mu$ . Politis has reported this fungus from Greece on *Muscari comosum* Mill.

21. Puccinia Allii (D.C.) Rud. Sacc. Syll. Fung. 7: 655; Politis, 1911; Sarejanni, 1935. (Figs. 20A, 20B.)

Collected at Thouria, Kalamai on March 17, 1939 (No. 61), on leaves of Allium sativum L. Uredospores were most prevalent,

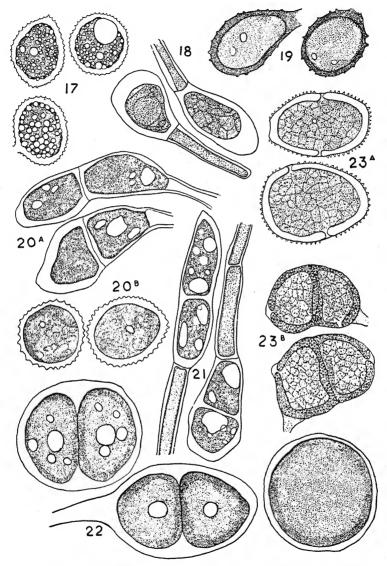


Fig. 17, Puccinia glumarum, uredospores; 18, Uromyces Junci, teleutospores; 19, Puccinia Polygoni-amphibii, uredospores; 20, Puccinia Allii, A, teleutospores, B, uredospores; 21, Puccinia Malvacearum, teleutospores; 22, Puccinia Asphodelii, teleutospores; 23, Puccinia Vincae, A, uredospores, B, teleutospores. All  $\times$  750.

but some teleutospores were also mature. Uredospores measure  $20.1\text{--}33.5 \times 15.5\text{--}28.5~\mu$  and teleutospores,  $41.5\text{--}57.5 \times 19.5\text{--}26~\mu$ .

22. Puccinia Asphodelii Daby. Sacc. Syll. Fung. 7: 666; Politis, 1911. (fig. 22.)

This fungus seems to be as common in Greece as its host. It was collected on Lykabettus Hill in Athens on March 9, 1939 (No. 52), by the writer, and at Koressia, Kea, on April 21, 1939 (No. 66), by Alexopoulou, on Asphodelus microcarpus Reichb. The latter specimen bears both uredospores and teleutospores. Measurements are: Uredospores,  $28.5-52 \times 20.5-28.5 \,\mu$ ; teleutospores,  $44-72 \times 33.5-52 \,\mu$ .

 Puccinia Glumarum (Schm.) Er. & Henn. Grove, British Rust Fungi, p. 258; Sacc. Syll. Fung. 17: 380; Politis, 1929; Sarejanni, 1935. (Fig. 17.)

Leaves of *Triticum vulgare* L. collected on March 17, 1939, at Sperchogia, Kalamai (*No. 60*), were heavily infected with the uredo stage of *P. glumarum*. Uredospores measure 20.5–28.5  $\times$  18–23.5  $\mu$ .

Puccinia Malvacearum Mont., Grove, British Rust Fungi,
 p. 206; Sacc. Syll. Fung. 7: 686; Politis, 1911; Sarejanni,
 1935. (Fig. 21.)

This fungus is widely distributed in Greece on a number of Malvaceous hosts. It was collected in December 1938 at Agia Paraskevi, Attica (No. 46), on leaves of Althea rosea L., and on February 27, 1939, back of the Institut at Drapetsona, Piraeus, on leaves of Malva rotundifolia L. (No. 51). Teleutospores, 41–68  $\times$  15.5–26  $\mu$ .

25. Puccinia Polygoni-amphibii Schroet. Grove, British Rust Fungi, p. 227. (fig. 19.)

This specimen was collected at Argos, Argolis, Zervos farm, on March 15, 1939 (No. 58). Only one leaf of Polygonum amphibium L. was found to be infected; it bore a considerable number of uredinia. The uredospores measure  $23.5-28.5 \times 21-26 \mu$ . They are thus, somewhat greater in diameter than those recorded

by Grove who gives  $25\text{--}28 \times 18\text{--}21~\mu$  as measurements for this species. No teleutospores were found.

26. Puccinia Vincae (D.C.) Plowright. Grove, British Rust Fungi, p. 176; Sacc. Syll. Fung. 9: 310; Politis, 1935; Sarejanni, 1935. (Figs. 23A, 23B.)

A rather common fungus on *Vinca major* L. collected at the Lakon garden, in Kephissia, Attica, on Oct. 30, 1938 (*No. 34*). Teleutospores measure  $32.5-45.5 \times 23.5-28 \mu$ .

# SPHAERIOIDACEAE

27. Phoma nebulosa (Pers.) Mont. Grove, British Stem & Leaf Fungi 1: 62; Sacc. Syll. Fung. 3: 135. (Fig. 25.)

This is the first report of this fungus from Greece. It was collected at Athens on Lykabettus Hill, on Dec. 11, 1938, on dried peduncles of *Asphodelus microcarpus* Reichb. (*No.* 43). Conidia,  $8-10.5 \times 3-4.5 \mu$ .

28. Phoma Viticis Celotti. Sacc. Syll. Fung. 10: 155; Politis, 1935.

A collection from Daphni, Attica, on leaves of *Vitex agnus-castus* L., taken on Nov. 5, 1938. The conidia from this specimen measure  $6.5\text{--}10.5 \times 2.5\text{--}5.5~\mu$  as compared with  $6\text{--}8 \times 2\text{--}3~\mu$  given by Saccardo for this species. The pycnidia are small and are brown instead of black as stated by Saccardo. Neither these differences, nor the fact that this was found on leaves, are considered by the writer as sufficient causes to separate this fungus from *Phoma Viticis*.

Septoria Piricola Desm. Grove, British Stem & Leaf Fungi
 400; Sacc. Syll. Fung. 3: 487; Politis, 1935. (Fig. 27.)

The conidial stage of *Mycosphaerella sentina* (Fries) Schr. commonly found in all pear growing districts of Greece causing considerable amount of damage to the leaves of pear trees. A collection was made at Argos, Argolis, on Sept. 19, 1938 (*No. 2*), and at Assini, Nauplia on the following day (*No. 3*). The conidia measure  $34-58 \times 3-4.5 \mu$ , thus exhibiting a greater variation than that reported by Grove  $(48-60 \times 3-4 \mu)$ .

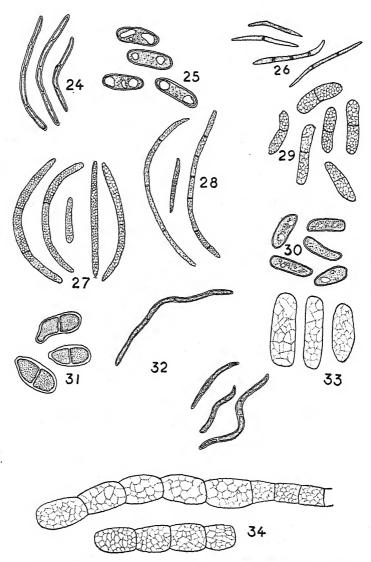


Fig. 24, Septoria pistacina, conidia; 25, Phoma nebulosa, conidia; 26, Septoria Urticae, conidia; 27, Septoria piricola, conidia; 28, Septoria Tritici, conidia; 29, Ascochyta Pisi, conidia; 30, Colletotrichum gloeosporioides, conidia; 31, Trichothecium roseum, conidia; 32, Septoria Unedonis, conidia; 33, Oidium Euonymi-japonici, conidia; 34, Oidium leucoconium, chains of conidia and portion of conidiophore. All ×750.

30. Septoria pistacina Allesch. Sacc. Syll. Fung. 16: 959; Politis, 1935; Sarajanni, 1935. (Fig. 24.)

This fungus, reported both by Politis and Sarejanni as occurring in Greece on *Pistacia vera* L. was collected by the writer on Oct. 16, 1938, on leaves of *Pistacia terebinthus* L., on Mt. Penteli, Attica (*No. 15*), and on leaves of a male tree of *P. vera* L., at Ekale, Attica, on Oct. 21, 1938 (*No. 18*). The conidia measure  $26-52 \times 1.5 \mu$ .

31. Septoria Tritici Rob. & Desm. Grove, British Stem & Leaf Fungi 1: 423; Sacc. Syll. Fung. 3: 561. (fig. 28.)

Specimens of diseased wheat plants were sent to the writer's laboratory at Piraeus for diagnosis of the disease, from Keramathika, Tyrnavos, Larissa. The sender claimed from 15 per cent to 25 per cent damage caused by this disease in the field in which these specimens were collected on March 24, 1939. The causal fungus was determined as *Septoria Tritici* (No. 65).

The conidia which are mostly 3-septate, measure  $46-66.5 \times 1-1.5 \, \mu$ . Grove gives  $60-65 \times 3.5-5 \, \mu$  as dimensions for the conidia of this fungus. He states, however, that "Cavara gives the typical spores of S. Tritici as  $50-60 \times 1.5-2 \, \mu$ ..." Neither Politis nor Sarejanni list this fungus as having been found by them in Greece. Sarejanni (Ann. Inst. Phytopath. Benaki 1, No. 2, p. 19, 1935) lists S. graminum on Triticum sp. from Greece. The measurements of the spores of the latter species, according to Grove (1: 421) are  $45-75 \times 1-1.5 \, \mu$ . This would fit the specimen on hand, but the spores of S. graminum are supposed to be aseptate or "rarely with a few indistinct septa" (Grove) while those of the specimen under discussion are distinctly septate. Because of this fact, it is believed that we are dealing with S. Tritici in the present case.

32. Septoria Unedonis Rob. & Desm. Grove, British Stem & Leaf Fungi 1: 369; Sacc. Syll. Fung. 3: 493; Sarejanni, 1935; Politis, 1938. (Fig. 32.)

Infected leaves of *Arbutus unedo* L. were collected on Mt. Penteli, Attica, on Oct. 16, 1938 (*No. 16*), and again at Bafi, Attica, on Oct. 25, 1938 (*No. 21*). The spores measure 17.5–

 $35 \times 1.5$ –2  $\mu$ . This species is apparently very variable in the size of its spores. Grove (1: 369) gives 25–30  $\times$  1.5–2  $\mu$  as measurements from a British specimen and 25–63  $\times$  2–3  $\mu$  from a Cyprian specimen.

Sarejanni (Ann. Inst. Phytopath. Benaki 1, No. 2, p. 13, 1935) reports S. Unedonis Rob. var. vellanensis Br. & Cav., as occurring on Arbutus  $unedo \times andrachne$  Bois, in Greece, and Politis (Pragm. Acad. Athènes, 3, No. 4, p. 33, 1935), describes a new species, S. andrachnes Pol., from Arbutus andrachne L., the conidia of which measure  $30-40\times 1-1.5~\mu$ . From the description given, it would appear that there is little difference between it and S. Unedonis and that the two are probably synonymous.

33. Septoria Urticae Desm. & Rob. Grove, British Stem & Leaf Fungi 1: 413; Sacc. Syll. Fung. 3: 557; Politis, 1935. (fig. 26.)

Collected at Argos, Argolis, near the ancient theatre, on Urtica pilulifera~(No. 55). The pycnidia measure 65–111  $\mu$  in diameter. Conidia, 30–50.5  $\times$  1–1.5  $\mu$ . Politis reports this species from Attica on leaves of Urtica~urcns. The spore measurements agree with those given by Grove.

34. Ascochyta Pisi Lib. Grove, British Stem & Leaf Fungi 1: 309; Sacc. Syll. Fung. 3: 397; Politis, 1935; Sarejanni, 1935. (Fig. 29.)

Leaves of *Vicia faba* L. infected with this fungus were brought to the writer's laboratory for diagnosis from Helleniko, Attica, in January 1939 (*No. 45*). Conidia,  $11-27.5 \times 4.5-6.5 \mu$ .

35. Coniothyrium concentricum (Desm.) Sacc. Grove, British Stem & Leaf Fungi 2: 14; Sacc. Syll. Fung. 3: 317; Sarejanni, 1935. (Fig. 39.)

This collection (*No. 13*) was made on Oct. 16, 1938. Sections of infected leaves of *Agave americana* L. growing by the side of the road leading from Amaroussion, Attica, to Mt. Penteli, were found to bear the pycnidia of this fungus. The conidia measure  $5-6.5 \times 5 \mu$ .

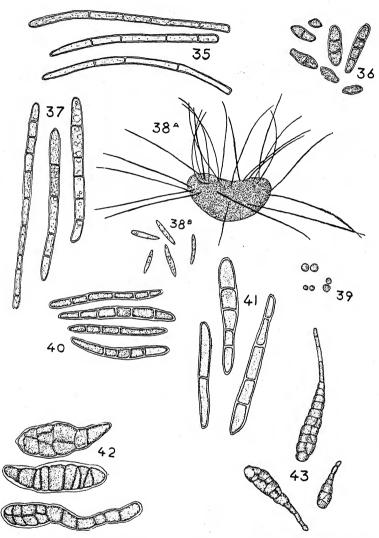


Fig. 35, Cercospora myrticola, conidia; 36, Cladosporium herbarum, conidia; 37, Cercospora smilacina, conidia; 38, Chaetomella atra, A, pycnidium, B, conidia; 39, Coniothyrium concentricum, conidia; 40, Cercospora neriella, conidia; 41, Cercospora Capparidis, conidia; 42, Macrosporium Vitis, conidia; 43, Alternaria Brassicae, conidia. Fig. 38 A, × 75, all others × 750.

36. CHAETOMELLA ATRA Fuckel, Sacc. Syll. Fung. 3: 321. (FIGS. 38A, 38B.)

Dried pedicels of *Papaver rhoeas* L. collected on Lykabettus Hill in Athens on Dec. 11, 1938, were found to bear pycnidia of *Chaetomella atra* Fuckel. The pycnidiospores measure  $13-15 \times 3 \mu$ . The pycnidia are either sphaerical or of the shope shown in figure 38A. This is the first report of the fungus from Greece (No. 44).

#### ZYTHIACEAE

37. POLYSTIGMINA RUBRA Sacc. Grove, British Stem & Leaf Fungi 2: 121; Sacc. Syll. Fung. 3: 622.

This is the imperfect stage of *Polystigma rubra* (Pers.) D.C., collected on leaves of *Amygdalus communis* L., on Mt. Penteli, Attica, Oct. 16, 1938 (*No. 14*). The conidia average  $24 \times 1.5 \mu$ . Sarejanni (Ann. Inst. Phytopath. Benaki 1, No. 2, p. 17, 1935) reports *Polystigma ochraceum* Sacc. on almond, in Greece.

## MELANCONIACEAE

38. Colletotrichum gloeosporioides Penz. Sacc. Syll. Fung. 3: 735; Politis, 1935, Sarejanni, 1935. (Fig. 30.)

Commonly found in all Citrus growing sections of Greece as the cause of withertip and as a secondary parasite, following other pathogens. This specimen (*No. 41*) was collected at Gargalianoi, Trifyllia in September 1938 by Mr. Papademetriou, on *Citrus sinensis* Osb. The conidia measure  $13-18.5 \times 5-7 \mu$ .

### MONILIACEAE

39. OIDIUM EUONYMI-JAPONICI (Archang.) Sacc. Syll. Fung. 18: 506; Politis, 1935; Sarejanni, 1936. (FIG. 33.)

Widely distributed as a parasite of *Evonymus japonicus* L. which is commonly used as an ornamental throughout Greece. The present specimen (*No. 1*) was collected at Kephissia, Attica, on Sept. 10, 1938. The conidia measure  $21.5-34.5 \times 9.5-15.5 \mu$ . Saccardo gives  $30-38 \times 13-14 \mu$  as conidial dimensions.

40. OIDIUM LEUCOCONIUM Desm. Sacc. Syll. Fung. 4: 41; Politis, 1935; Sarejanni, 1935. (FIG. 34.)

This fungus which causes considerable damage to peaches and roses, is quite common in Greece. It has been reported by Politis from rose and by Sarejanni from peach. The specimens on hand consist of infected peach leaves and young stems (No. 7) collected on Sept. 30, 1938, in the orchards of the Florina Agricultural School in Florina, and of infected leaves of Rosa sp. (No. 39) collected near Psychico, Attica, on Nov. 13, 1938. The conidia from peach leaves measure  $18-21 \times 8-13~\mu$ . These dimensions are smaller than  $20-30 \times 13-16~\mu$ , given by Saccardo for the same fungus.

41. OIDIUM MONILIOIDES Link. Sacc. Syll. Fung. 4: 46; Politis, 1935; Erysiphe graminis D.C., Politis, 1935; Sarejanni, 1935.

Collected at Argos, Argolis, near the ancient theatre, on *Triticum vulgare* L. (No. 53). The conidia, found in abundance, measure  $28-36.5 \times 8.5-13 \mu$ . Many perithecia, undoubtedly of *Erysiphe graminis* of which this is the conidial stage, had been formed at the time of collection, but none were mature. Both stages have been reported from Greece by Politis.

42. Botrytis cinerea Pers. Sacc. Syll. Fung. 4: 129; Politis, 1935; Sarejanni, 1935.

A collection from the Athanasopoulos vineyard at Ekale, Attica, where it was found to cause considerable damage to mature grape berries, taken on Oct. 21, 1938 (No. 17). Measurements for the conidia on fruits of Vitis vinifera L.,  $8.5-17 \times 8-11 \mu$ .

43. Trichothecium roseum (Pers.) Link. Sacc. Syll. Fung. 4: 178; Politis, 1935; Sarejanni, 1935. (Fig. 31.)

On leaves of *Vitis vinifera* L. collected at Gargalianoi, Trifyllia, on Oct. 25, 1938 (*No. 19*), and sent to the writer's laboratory. Conidia,  $15.5-24 \times 8.5-11 \mu$ .

## DEMATIACEAE

44. Cladosporium Herbarum (Pers.) Link. Sacc. Syll. Fung. 4: 350; Politis, 1935; Sarejanni, 1935. (fig. 36.)

A very common saprophyte. On scorched leaves of *Pistachia lentiscus* L., collected at Rema Loverthou, Kephissia, Attica, on Oct. 30, 1938 (*No.* 26). Conidia,  $5.5-19.5 \times 3.5-5 \mu$ .

45. Macrosporium Vitis Sorok, Sacc. Syll. Fung. 11:635. (fig. 42.)

This fungus, new to Greece, was found on diseased mature berries of *Vitis vinifera* L. on Nov. 9, 1938, at Bafi, Attica (*No.* 85). There is a large variation in the size of the conidia which were found to measure  $17-58.5 \times 10.5-18 \,\mu$ . Saccardo records 28-30  $\times$  15  $\mu$  for this species.

46. ALTERNARIA BRASSICAE (Berk.) Sacc. Syll. Fung. 4: 546; Politis, 1935. (Fig. 43.)

This fungus, reported from Greece by Politis on leaves of *Brassica oleracea* L., was collected on leaves of *Phaseolus vulgaris* L., on Sept. 21, 1938, at Agios Vasileios, Corinthia (*No. 4*), and on Sept. 30, 1938, at Florina, Macedonia (*No. 10*). A very large variation in the size of the conidia was observed, the measurements being  $42-121 \times 11-15.5 \,\mu$  as compared to  $60-80 \times 14-18 \,\mu$  given by Saccardo.

47. Cercospora Capparidis Sacc. Syll. Fung. 4: 435; Politis, 1935. (Fig. 41.)

Collected at Daphni, Attica, on Nov. 5, 1938, on leaves of *Capparis spinosa* L. (*No. 36*). The conidia measure  $26-82.5 \times 5-6.5 \mu$  and vary in septation from continuous to 8-septate.

48. Cercospora myrticola Speg. Sacc. Syll. Fung. 10: 643; C. myrti Erikss., Politis, 1935. (Fig. 35.)

Collected on Oct. 16, 1938, on Mt. Penteli, Attica, on leaves of Myrtus communis L. The conidia measure  $56-101.5 \times 3-5.5 \mu$ . The fungus was kindly identified by Prof. C. C. Chupp of Cornell University, to whom the writer is grateful.

49. Cercospora neriella Sacc. Syll. Fung. 4: 473. (fig. 40.)

Leaves of plants of Nerium Oleander L. growing wild at the bottom of a ravine at Rema Loverthou, near Kephissia, Attica, were found to be infected by this fungus (No. 27). The fructification appears on the upper side of the leaves on definitely limited spots, brownish when young, turning grayish white with age, and limited by a brown margin, in turn surrounded by an area of yellow discoloration of the adjoining leaf tissue. The conidiophores arise in stromatic masses which appear more or less globose under the binocular. The conidia are septate and vary greatly in size,  $26.5-70 \times 3.5-5 \mu$ . This very interesting fungus is for the first time being reported from Greece.

50. CERCOSPORA SMILACINA Sacc. Syll. Fung. 4: 476; Politis, 1911. (FIG. 37.)

A large number of leaves of *Smilax aspera* L. were found to be infected by this fungus. This specimen (*No. 25*) was collected at Rema Loverthou, near Kephissia, Attica, on Oct. 30, 1938. The fungus has also been observed by the writer in many other places in Greece where *Smilax aspera* grows abundantly.

PHYTOPATHOLOGICAL LABORATORIES.

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#### UREDINALES OF NEW GUINEA<sup>1</sup>

George B. Cummins 2

(WITH 14 FIGURES)

The 34 species of Uredinales reported in this paper were collected by Mrs. Mary Strong Clemens in Morobe District, New Guinea. Of these 34 species 20 are described as new, with two serving as the basis for a new genus. The type specimens are deposited in the Arthur Herbarium, Purdue University Agricultural Experiment Station.

#### Puccinia mera sp. nov. (FIG. 10)

Urediis amphigenis, rotundatis vel ovoideis, 0.1-0.3 mm. longis, brunneis, sparsis; urediosporis late ellipsoideis vel obovoideis,  $17-23 \times 23-29 \,\mu$ ; membrana  $1.5 \,\mu$  cr., cinnamomeo-brunnea, moderate echinulata, poris germ. 2, aequatorialibus. Teliis urediis conformibus; teliosporis oblongo-ellipsoideis vel clavatis, ad apicem rotundatis, ad basim plerumque attenuatis, medio constrictis,  $13-17 \times 37-53 \,\mu$ ; membrana  $1-1.5 \,\mu$  cr., ad apicem  $5-8 \,\mu$ , aureo- vel castanco-brunnea, levi; pedicello hyalino, sporam subaequante.

On *Schoenus* aff. *subaxillaris* Kukenth., Mt. Sarawaket, Apr. 14, 1939 (10131bis); Samanzing vicinity, Dec. 22, 1938 (10398bis); Upper Camp, Feb. 21, 1939 (9879); Mt. Sarawaket, June 8, 1939 (s.n., type).

The apical thickening of the teliospores becomes paler terminally and has somewhat the appearance of a differentiated umbo.

## Puccinia oblongatoides sp. nov. (FIG. 1)

Urediis amphigenis, maculis rufo-brunneis insidentibus, ellipticis vel oblongis, 0.2–0.5 mm. longis, sparsis, cinnamomeo-brunneis; urediosporis obovoideis vel oblongo-ellipsoideis,  $12-17 \times 23-29 \,\mu$ ; membrana  $0.5-1.0 \,\mu$  cr., hyalina, levi, poris germ. obscuris (nullis?). Teliis urediis conformibus sed

- <sup>1</sup> Contribution from the Department of Botany, Purdue University Agricultural Experiment Station, Lafayette, Indiana.
- <sup>2</sup> I am much indebted to the following persons for giving opinions concerning the identity of some of the hosts: Drs. S. F. Blake, H. D. House, I. M. Johnston, E. D. Merrill, H. N. Moldenke, G. L. Stebbins, Jr., and H. K. Svenson.

castaneo-brunneis; teliosporis oblongis vel clavatis, ad apicem rotundatis vel obtusis vel leniter attenuatis, ad basim attenuatis, medio constrictis,  $13-17 \times 38-50 \,\mu$ ; membrana  $1-1.5 \,\mu$  cr., ad apicem  $5-8 \,\mu$ , castaneo-brunnea; pedicellis fulvis, usque ad  $30 \,\mu$  longis.

On Lusula sp., Mt. Sarawaket, Apr. 22, 1939 (s.n., type); Upper Camp, Feb. 21, 1939 (s.n.).

This species is closely related to *P. oblongata* (Lk.) Wint. but is readily distinguishable because of the smaller urediospores and teliospores.

## Puccinia citricolor sp. nov. (FIG. 3)

Pycnia amphigena, subepidermalia, globosa, paraphysata,  $100-135\,\mu$  diam. Aeciis amphigenis in maculis incrassatulis usque ad 15 mm. diam. profunde immersis, pallide flavidis, 0.2-0.3 mm. diam.; cellulis peridii laxe conjunctis, oblongo-ellipsoideis vel oblongis  $25-40\times45-75\,\mu$ , pariete interiore rugoso  $3\,\mu$  cr., exteriore levi  $2\,\mu$  cr.; aeciosporae late ellipsoideae vel oblongo-ellipsoideae,  $28-40\times39-55(-60)\,\mu$ ; membrana flavida verrucoso-rugosa  $3-6\,\mu$  cr., ad apicem  $8-18\,\mu$ . Uredia hypophylla, subepidermalia, flavida, sparsa vel laxe aggregata,  $0.1-0.7\,$  mm. diam.; urediosporae obovoideae,  $24-30\times33-50\,\mu$ ; membrana flavida  $2.5-4\,\mu$  cr., ad apicem  $4-12\,\mu$ , valde aculeata, poris germ. obscuris. Telia hypophylla, subepidermalia, in maculis atro-brunneis usque ad 15 mm. diam. dense aggregata, flavida vel brunnea; teliosporae ellipsoideae, oblongo-ellipsoideae vel clavatae, utrinque rotundatae vel ad basim attenuatae, medio constrictae,  $18-26\times39-60\,\mu$ ; membrana flavida  $2\,\mu$  cr. vel ad apicem  $2.5-3.5\,\mu$ ; pedicellis concoloris  $8-12\times10-20\,\mu$ . Statim germ.

On *Smilax* sp., Sattelberg, Nov. 18, 1935 (902), Nov. 30, 1935 (1038, type); Yunzaing, Apr. 25, 1936 (2958), June 11, 1936 (3276), July 1, 1936 (3484), July 17, 1936 (s.n.), Aug. 12, 1936 (3886bis), Aug. 21, 1936 (s.n.).

Puccinia citricolor differs from the previously described species of Puccinia on Smilax because of the non-inflated, short and usually largely deciduous pedicels and the nearly uniform wall of the teliospores. All four spore stages are present in the type, pycnia, aecia and telia in no. 902 and telia in the remaining collections. The close association of the aecia and telia and the presence of teliospores in the uredia indicate that all belong to a single species.

Mrs. Clemens notes the rust as "yellow" and in dried specimens the young sori remain yellowish with an olivaceous tint which changes with age to sordid brown. The greenish tint in the teliospores is conspicuous microscopically. PUCCINIA CONGESTA Berk. & Br.

On *Polygonum chinense* L., Yunzaing, Apr. 25, 1936 (2949), Aug. 20, 1936 (3933A); vicinity of Milulunga, July 6, 1939 (10430).

#### Puccinia aegroides sp. nov. (FIG. 4)

Pycniis ignotis. Aeciis plerumque hypophyllis, totam folii superficiem occupantibus, cupulatis; cellulis peridii  $15-21\times23-30\,\mu$ ; membrana rugosa  $3\,\mu$  cr.; aeciosporis globosis,  $11-16\times13-18\,\mu$ ; membrana  $0.5-1\,\mu$  cr., subtiliter verruculosa. Urediis amphigenis, rotundatis, 0.1-0.3 mm. diam., pallide cinnamomeis; urediosporis oblongo-ellipsoideis, ellipsoideis vel obovoideis,  $14-21\times23-34\,\mu$ ; membrana  $2\,\mu$  cr., flavida vel pallide cinnamomeo-brunnea, echinulata, poris germ. 2, aequatorialibus. Teliis urediis conformibus sed castaneis; teliosporis variabilis, oblongis, ellipsoideis vel late ellipsoideis, ad apicem rotundatis, ad basim attenuatis vel rotundatis, medio non vel leniter constrictis,  $15-20\times24-35\,\mu$ ; membrana  $1.5\,\mu$  cr., apice  $3-5\,\mu$  et papillata, in cellulis apicalis subtiliter verrucosa: pedicello hyalino, brevi.

On Viola sp., Upper Camp A, Mar. 1939 (10006); Mt. Sarawaket, Apr. 14, 1939 (s.n.), Apr. 17, 1939 (s.n., type), June 8, 1939 (s.n.).

This rust is closely related to *P. aegra* Grove but differs because of longer urediospores and apically verrucose teliospores. Both lack pycnia, both have systemic aecia and in both the pore in the lower cell of the teliospore is at the septum.

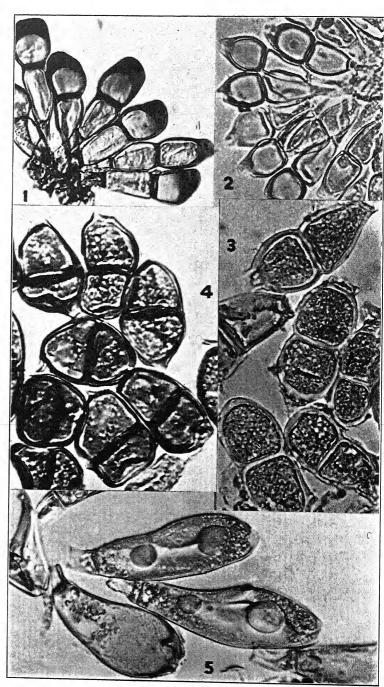
# PUCCINIA HALORAGIDIS Sydow

On *Haloragis micrantha* R. Br., vicinity of Samanzing, Nov. 22–23, 1938 (9361), Dec. 22, 1938 (s.n.); Upper Camp, Feb. 19, 1939 (9844).

Teliospores present in no. 9844 are somewhat smaller than those in the Japanese specimens at my disposal but fall within the range given in the original description. The species is scarcely distinct morphologically from the North American *P. Proserpinacae* (Berk. & Curt.) Farl.

# Puccinia morobeana sp. nov. (FIG. 2)

Urediis hypophyllis, subepidermicis, brunneis, rotundatis vel ovatis, 0.1–0.5 mm.; urediosporis globoideis vel late ellipsoideis,  $16-20\times19-24\,\mu$ ; membrana cinnamomea  $1.5\,\mu$  cr., poris germ. 2, aequatorialibus. Teliis conformibus; teliosporis clavatis vel oblongo-clavatis, ad apicem rotundatis vel leniter attenuatis, ad basim attenuatis, medio leniter constrictis,  $11-16\times31-42(-47)\,\mu$ ; membrana aureo-brunnea  $1-1.5\,\mu$  cr., ad apicem  $3-7\,\mu$ , levi; pedicello hyalino, sporam aequante vel breviore, fragili.



Figs. 1-5.

On Gentiana aff. Ettinghausenii F. Muell., Mt. Sarawaket, May 1939 (s.n.), June 8, 1939 (10235, type). On Gentiana near Mac Gregorii Hemsl., Upper Camp A, Apr. 10, 1939 (10117G); Mt. Sarawaket, June 8, 1939 (10235B), June 15, 1939 (10247B).

Puccinia morobeana is similar to P. Cockaynei G. H. Cunn. but has narrower and lighter colored teliospores.

#### Puccinia Ixeridis sp. nov. (FIG. 12)

Pycniis hypophyllis, totam folii superficiem occupantibus, subepidermicis, globosis,  $115-165\,\mu$  diam. Aeciis inter pycnia sparsis, cupulatis, 0.2-0.35 mm. diam., cellulis peridii rhomboideis vel ellipsoideis,  $16-21\times25-30\,\mu$ , pariete interiore rugoso  $3-6\,\mu$  cr., exteriore verruculoso  $1\,\mu$  cr.; aeciosporae late ellipsoideae vel oblongo-ellipsoideae,  $13-18\times19-26\,\mu$ ; membrana hyalına verruculosa  $1\,\mu$  cr. Urediis epiphyllis, flavidis, minutis, 0.1-0.2 mm. diam., sparsis; urediosporae obovoideae, late ellipsoideae vel globosae,  $15-19\times18-22\,\mu$ ; membrana pallide flavida vel hyalina  $1-1.5\,\mu$  cr., moderate echinulata, poris germ. aequatorialibus, 3. Teliis conformibus sed brunneis; teliosporae ellipsoideae vel late ellipsoideae, utrinque rotundatae, medio leniter constrictae,  $24-30\times34-40\,\mu$ ; membrana  $1-1.5\,\mu$  cr., pallide castaneo- vel aureo-brunnea, levi; poro superiore subapicali, inferiore infra medium loculum sito; pedicello hyalino, fragili, mox deciduo.

On Ixeris papuana (S. Moore) Stebbins, vicinity of Samanzing, Feb. 1939 (ex 9871bis, type), Upper Camp A, Mar. 1939 (s.n.); on Ixeris umbellata (Mattf.) Stebbins, Upper Camp, Feb. 17, 1938 (9831).

It is impossible with the available material to be certain that the aecia actually belong with the uredia and telia but their apparent association favors this view. The specimen taken as the type was segregated from no. 9871bis which is also taken as the type of *P. ixeridicola*, but the latter is obviously a microcyclic species and has no connection with the aecia.

## Puccinia ixeridicola sp. nov. (FIG. 13)

Pycnia, aecia et uredia nulla. Telia subepidermalia amphigena, brunnea, pulvinata, rotundata, dense aggregata in maculis 1–3 mm. diam.; teliosporae oblongae vel clavatae, ad apicem rotundatae vel attenuatae, ad basim attenuatae, medio non vel vix constrictae,  $10-15 \times (23-)29-40 \,\mu$ ; membrana hyalina vel pallide flavida,  $1 \,\mu$  cr., ad apicem  $3-6 \,\mu$  cr., levi; pedicello hyalino, sporam aequante vel breviore. Statim germ.

Fig. 1, teliospores of Puccinia oblongatoides on Luzula (×650); 2, teliospores of Puccinia morobeana on Gentiana (×700); 3, teliospores of Puccinia citricolor on Smilax (×725); 4, teliospores of Puccinia aegroides on Viola (×900); 5, teliospores of Uromyces permeritus on Tournefortia (×750).

On *I.veris papuana* (S. Moore) Stebbins, vicinity of Samanzing, Feb. 1939 (9871bis, type), Upper Camp A, Mar. 1939 (s.n.).

UROMYCES AFFINIS Wint.

On *Hypoxis* sp., Malalo Mission, May 27, 1936 (3148); Kajabit Mission, July 24, 1939 (10475).

Only uredia are present in these collections but they differ in no way from the uredia of American specimens of U. affinis.

## Uromyces permeritus sp. nov. (FIG. 5)

Pycniis epiphyllis, subepidermalibus,  $130-150~\mu$  latis,  $165-200~\mu$  altis, maculis incrassatulis usque 3 mm. diam. occupantibus. Aeciis uredinoidibus, amphigenis, inter pycnia sparsis, cinnamomeo-brunneis, plus minusve profunde immersis,  $150-300~\mu$  diam.; aeciosporae obovoideae,  $20-30~\times~36-56~\mu$ ; membrana  $2~\mu$  cr., ad apicem  $3-6~\mu$ , cinnamomeo-brunnea, valde echinulata, poris germ. 3, aequatorialibus. Urediis hypophyllis, subepidermalibus, sparsis vel laxe aggregatis, cinnamomeo-brunneis, 0.1-0.2~mm. diam.; urediosporis aeciosporis conformibus. Teliis urediis conformibus; teliosporae oblongo-ellipsoideae,  $20-26~\times~42-66~\mu$ ; membrana flavida vel aureo-brunnea, levi,  $1~\mu$  cr., ad apicem  $3-6~\mu$ ; pedicellis flavidis, usque  $16~\mu$  latis, sporam aequante vel longiore.

On Tournefortia probably sarmentosa Lam., above Boana, Aug. 23, 1938 (8702).

The apical thickening of the teliospores consists of a hyaline papilla which disappears during germination and, since the spores germinate immediately, is apt not to be seen. *U. dolichosporus* D. & H. is a similar species but has smaller spores.

UROMYCES WEDELIAE P. Henn.

On Wedelia biflora (L.) DC., Malalo Mission, Salamaua, Aug. 22, 1935 (11); Sattelberg, Jan. 25, 1936 (1376); Mosum to Lae, July 7, 1939 (s.n.).

UROMYCES BIDENTICOLA (P. Henn.) Arth.

On *Bidens* sp., Sattelberg, Sept. 20, 1935 (162), Oct. 1935 (s.n.); Yoangen Village, June 18, 1936 (3380); Wau, July 19, 1939 (10456V).

# Corbulopsora gen. nov. (Pucciniaceae)

Pycnia subepidermalia, paraphysata. Aecia subepidermalia, cupulata, peridio praedita; aeciosporae catenulatae. Uredia telia conformibus; uredio-

sporae pedicellatae, echinulatae, poris germ. instructae. Telia subepidermalia, erumpentia, peridio valliforme cincta; teliosporae unicellulares solitarie in apice pedicelli natae, apice poro germinationis unico instructae.

Type species: Corbulopsora Clemensiae Cumm.

## Corbulopsora Clemensiae sp. nov. (Fig. 6, 7, 9)

Pycnia epiphylla, profunde immersa, globosa,  $180-250\,\mu$  diam. Aecia epiphylla, profunde immersa, in maculis brunneis laxe aggregata, cupulata, 0.4–0.6 mm. lata, 0.3–0.5 mm. alta; cellulis peridii oblongis vel rhomboideis,  $20-45\times55-90\,\mu$ , pariete interiore verrucoso  $8-11\,\mu$  cr., exteriore striato  $2\,\mu$  cr.; aeciosporae oblongo-ellipsoideae vel late ellipsoideae,  $25-44\times39-55\,\mu$ ; membrana hyalina vel pallide flavida,  $3.5-6\,\mu$  cr., valde verrucosa. Uredia hypophylla subepidermalia, cylindracea,  $100-200\,\mu$  lata,  $165-250\,\mu$  alta; peridio valliformi ex cellulis  $13-30\times130-165\,\mu$  composito; membrana flavo-brunnea  $2-3\,\mu$  cr.; urediosporae late ellipsoideae vel obovoideae,  $33-40\times39-55\,\mu$ ; membrana hyalina vel pallide flavida,  $3.5-5\,\mu$  cr., valde echinulata, poris germ. 6-8, sparsis instructa. Telia uredia conformibus sed castanea; teliosporae cylindraceae vel oblongo-cylindraceae, ad apicem rotundatae vel obtusatae, ad basim leniter attenuatae,  $23-32\times80-112\,\mu$ ; membrana aureovel castaneo-brunnea,  $1.5\,\mu$  cr., ad apicem  $9-13\,\mu$ , levi; pedicello hyalino, sporam aequante vel longiore. Statim germ.

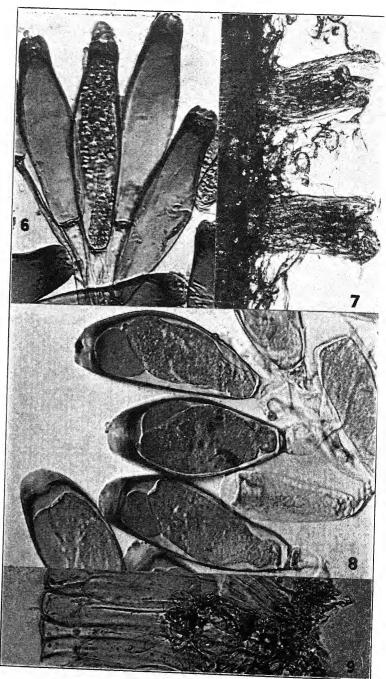
On *Olearia* sp., vicinity of Samanzing, Dec. 30, 1939 (10341), Feb. 1939 (9690V, type).

## Corbulospora gravida sp. nov. (fig. 8)

Pycnia epiphylla subepidermica, profunde immersa, globosa,  $190-275~\mu$  diam. Aecia hypophylla, profunde immersa, plus minusve sparsa vel in maculis brunneis laxe aggregata, cupulata vel cylindracea, 0.3-0.5 mm. lata, 0.4-0.8 mm. alta; cellulis peridii oblongis vel rhomboideis,  $25-40\times50-75~\mu$ ; pariete interiore verrucoso  $5-8~\mu$  cr., exteriore striato  $1.5~\mu$  cr.; aeciosporae ellipsoideae vel oblongo-ellipsoideae,  $25-39\times50-75~\mu$ ; membrana hyalina  $2-2.5~\mu$  cr., valde verrucosa. Uredia ignota. Telia hypophylla, subepidermica, pulvinata vel cylindracea,  $100-165~\mu$  lata,  $175-250~\mu$  alta; peridio valliformi ex cellulis  $15-25\times100-150~\mu$  composito; membrana flavida  $3-5~\mu$  cr.; teliosporae ellipsoideae vel oblongo-ellipsoideae, ad apicem rotundatae, ad basim attenuatae,  $30-42\times70-105~\mu$ ; membrana aureo-brunnea  $1.5-2~\mu$  cr., ad apicem  $8-12~\mu$  cr., levi; pedicello hyalino, sporam aequante. Statim germ.

On *Olearia* sp., vicinity of Samanzing, Jan. 7, 1939 (10369); Mt. Sarawaket, Apr. 1939 (10117N), May 1939 (s.n., type).

The rusts described here as *Corbulopsora Clemensiae* and *C. gravida* are considered to have morphological features sufficiently distinctive to require segregation in a new genus. Both species have large teliospores with the characteristics of those of the genus



Figs. 6-9.

Uromyces but the spores are produced within an encircling peridium composed of long, slender, palisade-like cells united laterally.

The peridial cells and aeciospores of both species are large and more reminiscent of those found in such genera as *Coleosporium* and *Chrysomyxa* than of those usual in *Uromyces*. Their walls are coarsely sculptured with rather large tubercles which have an irregular and more or less stellate outline. In *C. gravida* the tubercles are somewhat deciduous, slightly smaller and borne on a thinner wall than in *C. Clemensiae*.

Uredia are known only for *C. Clemensiae* and are produced within the same stockade-like peridium as are the teliospores, or the teliospores may develop in the uredia. The teliospores are of approximately the same length in both species but those of *C. Clemensiae* are significantly narrower. Both germinate at once.

#### Sphaerophragmium boanense sp. nov. (FIG. 14)

Teliis maculis brunneis usque ad 5 cm. diam. insidentibus, hypophyllis, subepidermicis, dense aggregatis, brunneis,  $150-250~\mu$  diam., primo epidermide tectis, dein poro rotundo apertis; teliosporis globosis, ellipsoideis vel oblongis, cinnamomeis, ex cellulis 3–7 compositis, superficie tuberculis brunneis hemisphaericis, conicis vel truncatis obsitis,  $25-39\times39-49~\mu$ ; episporio  $1.5~\mu$  crasso, poris germ. obscuris; pedicello sporam circiter aequante vel plerumque breviore, dilute colorato.

On Anonaceae, Boana, July 6, 1938 (8413).

Of the three infected leaves in this collection one has a spot 3 cm. in diameter, in the second the apical one-third (about 5 cm.) of the leaf is involved, while the entire third leaf is uniformly occupied by sori. The third leaf may indicate a locally systemic mycelium.

Sphaerophragmium boanense is related to S. Chevalieri Har. and Pat. but differs in causing larger infected areas in which the sori are hypophyllous rather than epiphyllous. The telia are smaller and the sculpture on the teliospores is more regularly tuberculate.

Fig. 6, teliospores of Corbulopsora Clemensiae on Olearia (× 550); 7, telia of Corbulopsora Clemensiae with a few urediospores; note the surrounding palisade-like peridia (× 125); 8, teliospores of Corbulopsora gravida on Olearia (× 550); 9, a portion of the telial peridium of Corbulopsora Clemensiae separated out to show the long laterally united peridial cells (× 425).

## Hamaspora acutissima Sydow

On Rubus diclinia F. Muell., vicinity of Samanzing, Dec. 30, 1938 (10343). On Rubus moluccanus L., Sattelberg, Sept. 20 1935 (116). On Rubus sp., between Sattelberg and Quembung, Dec. 13, 1935 (1121), Dec. 18, 1935 (s.n.); Samanzing, June 28, 1939 (10381).

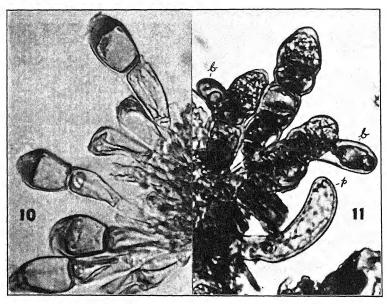


Fig. 10, teliospore of *Puccinia mera* on *Schoenus* ( $\times$  750); 11, portion of a crushed and stained telium of *Kuchncola papuana* on *Rubus* showing three teliospores, two with one basidial initial (b) each, and one paraphysis (p) ( $\times$  900).

Uredia could be found on only one collection but the long cylindrical telial paraphyses as well as the size and septation of the teliospores indicate H. acutissima. Since the uredia of Hamaspora often furnish more distinctive characters than do the uredia, as in H. acutissima and H. benguetensis Sydow, it may be that more than a single species is involved. The uredia mentioned above agree fairly well with those of H. acutissima but they are without accompanying telia.

#### Kuehneola papuana sp. nov. (Fig. 11)

Pycnia et aecia ignota. Uredia subepidermalia, hypophylla, flavida, pulverulenta, 0.1–0.3 mm. diam.; paraphysibus ad marginem sori evolutis, ad basim coalitis, cylindraceis, curvatis, 8– $10 \times 35$ – $50 \,\mu$ ; membrana hyalina,  $1 \,\mu$  cr.; urediosporae obovatae, 13– $16 \times 17$ – $25 \,\mu$ ; membrana hyalina vel pallide flavida, 1– $1.5 \,\mu$  cr., dense minuteque echinulata, poris germ. 4–6, sparsis. Telia uredia conformibus sed compacta; teliosporae clavatae vel cylindricoclavatae, 1–5 septatae, ad septa non vel leniter constrictae, apice rotundatae vel leniter attenuatae, 13– $16 \times 42$ – $50 \,\mu$ ; membrana hyalina 1– $1.5 \,\mu$  cr., ad apicem usque  $3 \,\mu$ , levi; pedicello brevissimo. Statim germ.

On Rubus papuanus Schltr. vel aff., Mt. Sarawaket, May 1939 (10216).

Adequate numbers of uredia are present in this collection but telia are rare and only one good mount was obtained. Certain features of the teliospores are not in accord with the characters of the genus Kuehneola. The cells of the teliospores are firmly united and give no impression of being catenulately produced, although the early stages of septation were not observed. Moreover, there is no indication of the presence of germ pores. Germination occurs at varying locations in the cells by the production of an outgrowth of the wall. The wall of the structure thus produced is of the same thickness as that of the teliospore and is continuous with it. The protoplasm moves into this outgrowth, which has a diameter nearly equal to that of the teliospore cell, and is then walled off by the formation of a septum about  $6 \mu$  distant from the teliospore. By this septation a terminal cell with an approximate size of  $10 \times 14 \,\mu$  is formed, with the original thickness of the wall retained. This terminal cell is presumably the basidium (Fig. 11, b) but, despite careful study, its further development could not be determined. It may be assumed, however, that the basidial initial by continued differentiation produces septae, sterigmata and basidiospores.

Paraphyses (FIG. 11, p), reminiscent of those found in some species of *Phragmidium* and of *Hamaspora*, are present around both the uredia and the telia. *Kuehneola*, as delimited by Dietel (E. & P. Nat. Pfl. 6: 60. 1928), does not form paraphyses and is restricted to rosaceous hosts. He places similar but paraphysate species which parasitize hosts belonging in families other than the Rosaceae in *Cerotelium*. The status of these two genera is con-

fused and the discovery of the rosaceous but paraphysate *K. papu*ana further complicates the situation.

The presence or absence of paraphyses is not generally considered to be especially significant in the characterization of genera of the Uredinales. Certainly such usage cannot be consistently adopted. Structurally, the teliospores of *K. papuana* differ somewhat, however, from those of other species of *Kuehneola*. The thick-walled basidial initial is unusual. Certainly the species is not a *Cerotelium*. Perhaps it is generically distinct and deserving of a position intermediate between *Kuehneola* and *Hamaspora* but without adequate telial material it seems inadvisable to introduce a new genus.

## CEROTELIUM FICI (Cast.) Arth.

On *Ficus* sp., Sattelberg, Dec. 6, 1935 (1204), Dec. 17, 1936 (1226); Heldsbach, Jan. 31, 1936 (1740); Malalo Mission, Salamaua, May 25, 1936 (3159); Yunzaing, July 17, 1936 (3605A); Samanzing to Milulunga, July 5, 1939 (10431).

## BUBAKIA EHRETIAE (Hirats.) S. Ito

On *Ehretia* sp., Sattelberg, Oct. 23, 1935 (575), Nov. 18, 1935 (920); Quembung trail, Dec. 9, 1935 (1175); Wareo, Dec. 25, 1935 (1361); Heldsbach to Sattelberg, Jan. 31, 1936 (1751); Butaweng saw mill, Mar. 18, 1936 (2101); Sattelberg, Wareo trail, Feb. 18, 1938 (s. n.).

Small (45–65  $\mu$  diam.) hemispherical or conical, subcuticular pycnia accompanied by uredinoid aecia, with spores like the urediospores, are present in no. 1175 in close association with uredia and telia. There is no reason to doubt that the primary and secondary stages belong to a single species. In addition to localized infection of the leaves the rust also is capable of infecting and causing hypertrophy of the fruits (no. 920). Sections of the fruits prove the uredia to be almost as frequent internally as externally.

# Рнакорsora теста Jackson & Holway

On Commelina sp., Sattelberg, Oct. 19, 1935 (506); vicinity of Milulunga, July 5, 1939 (10430bis).

#### Crossopsora Clemensiae sp. nov.

Pycnia subcuticularia, maculis leniter incrassatulis 1–3 mm. diam. occupantibus, hypophylla, hemisphaerica, 85–115  $\mu$  diam. Aecia hypophylla, inter pycnia sparsa, profunde immersa, peridio destituta, 130–215  $\mu$  diam.; aeciosporae ellipsoideae,  $16-20\times22-25\,\mu$ ; membrana hyalina,  $1.5\,\mu$  cr. vel ad apicem leniter incrassata, moderate echinulata. Uredia ignota. Telia hypophylla, subepidermalia, laxe aggregata, brunnea,  $100-250\,\mu$  diam.,  $80-120\,\mu$  alta; teliosporae oblongae,  $13-16\times18-22\,\mu$ ; membrana hyalina,  $1\,\mu$  cr.

On Glochidion sp., Boana, Aug. 13, 1938 (8622bis).

Crossopsora Clemensiae is readily distinguishable from C. Sawadae (Sydow) Arth. & Cumm. because the telia are not horn-like

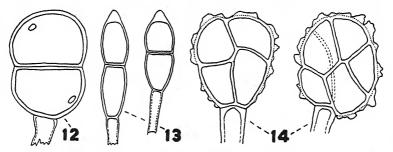


FIG. 12, one teliospore of *Puccinia Ixeridis* on *Ixeris*; 13, two teliospores of *Puccinia ixeridicola* on *Ixeris*; 14, two teliospores of *Sphaerophragmium boanense* on Anonaceae (×650).

but only erumpent-pulvinate and originate beneath the epidermis rather than deep within the mesophyll. Although the telia are not filiform *Crossopsora* seems the logical genus in which to place this species. The aecia, although old, are obviously like those of *C. Sawadae* and, without accompanying telia, could not well be distinguished. In this collection they are so closely associated with the telia, however, that they certainly are genetically related.

Crossopsora Sawadae (Sydow) Arth. & Cumm.

On *Glochidion* sp., Boana, June 4, 1938 (8325); Abe, Sarawaket, June 15–18, 1938 (8326); above Boana, Aug. 26, 1938 (s. n.); Kajabet Mission, July 27, 1939 (10482a).

There are three rusts known on Glochidion in New Guinea. For a discussion of the differences see Crossopsora Clemensiae and Aecidium foederatum.

Crossopsora Malloti (Racib.) comb. nov. (Cronartium Malloti Racib., Parasit. Algen Pilze Javas I, p. 23, 1900; Uromyces Malloti P. Henn., Engl. Bot. Jahrb. 15: 4. .1892; Uredo Malloti P. Henn., Vestergr. Micr. Rar. Sel. 870. 1905).

On *Mallotus* sp., Boana, May 6, 1938 (8192); Kajabit Mission, Aug. 15, 1939 (10577).

Because the uredia have septate peripheral paraphyses rather than a peridium this species is best referred to the genus *Crossopsora*.

UREDO ARTOCARPI Berk. & Br.

On Artocarpus sp., Sattelberg, Dec. 6, 1935 (1117A), Dec. 24, 1935 (s. n.); Quembung Mission, Mar. 19 and 23, 1936 (2140).

#### Uredo falcifera sp. nov.

Urediis subepidermalibus, hypophyllis, sparsis, brunneis, pulverulentis; paraphysibus periphericis copiosis, inferne conjunctis, plerumque falciformis, castaneo-brunneis,  $6\text{--}12\times25\text{--}55\,\mu$ ; membrana  $2\,\mu$  cr.; urediosporae plerumque obovoideae,  $14\text{--}18\times(19\text{--})23\text{--}30\,\mu$ ; membrana aureo- vel cinnamomeo-brunnea  $1\,\mu$  cr., moderate echinulata, poris germ. obscuris.

On Rubus Macgregorii F. Muell., Mt. Sarawaket, June 6, 1939 (10222).

Telia could not be found among the relatively abundant uredia but the species will probably be found to belong in *Hamaspora*. The uredia, judging by the description, of *H. Rubi-Sieboldii* (Kawagoe) Dietel are much like those of *U. falcifera* but with less typically sickle-shaped paraphyses. In gross appearance, intensity of the pigmentation and in the general shape of the paraphyses the sori of *U. falcifera* are like the uredia of *H. benguetensis* Sydow but the spores of the latter are shorter and thus more rotund.

## Uredo morobensis sp. nov.

Uredia subepidermalia amphigena, pulverulenta, rotundata vel ovoidea, 0.1–0.4 mm. diam. cinnamomea; urediosporae late ellipsoideae vel globoideae,  $16-20\times 20-23$  (-26)  $\mu$ ; membrana cinnamomeo-brunnea 1–1.5  $\mu$  cr., moderate echinulata, poris germ. 2, aequatorialibus.

On *Cerastium* probably *papuanum* Schltr., Mt. Sarawaket, Mar. 15, 1939 (10023, type), Apr. 14, 1939 (10135), Apr. 18, 1939 (10153).

UREDO CALLICARPAE Petch.

On Callicarpa pedunculata R. Br., Wareo, Dec. 26, 1935 (1368), Jan. 2, 1936 (1452, 1453); Yunzaing, June 12, 1936 (3264A), July 16, 1936 (s. n.).

Epiphyllous, subcuticular, conical pycnia  $100-135\,\mu$  in diameter are present in no. 1452, encircled by amphigenous, subepidermal, paraphysate uredinoid aecia. The aecia are like the uredia except that the septate paraphyses are somewhat smaller. The aeciospores agree in size, color and echinulation with the urediospores and the two stages undoubtedly belong together.

#### UREDO CUMULA Arth.

On Buchnera probably urticifolia R. Br., Salamaua, May 25, 1936 (3141).

It is remarkable that this species, previously known only from the type specimen collected in Cuba, should be found in New Guinea but the pulverulent uredia are the same bright cinnamonbrown and the urediospores are indistinguishable. The specimen is only scantily infected.

# Uredo adapertilis sp. nov.

Uredia hypophylla, subepidermalia, laxe gregaria, rotundata, brunnea, 130–200  $\mu$  diam.; urediosporae obovoideae, ellipsoideae vel oblongo-ellipsoideae, 18–24  $\times$  29–39  $\mu$ ; membrana flavida, moderate echinulata, 1–1.5  $\mu$  cr., poris germ. obscuris, 5–7 aequatorialibus instructa.

On *Erechtites haplogynus* (F. Muell.) Mattf. vel aff., Marsh Meadow Camp, Dec. 22, 1938 (s. n., type); vicinity of Samanzing, Jan. 1939 (s. n.).

The sori are lenticular in section and open by an irregular and rather small aperture. The germ pores seem to be large but nevertheless are too obscure to count with accuracy.

#### UREDO MICROGLOSSAE Petch.

On Microglossa volubilis (Wall.) DC., Wareo, road to Heldsbach, Jan. 10, 1936 (1610); Yunzaing, June 1, 1936 (3277A); Yoangen, June 18, 1936 (s. n.).

#### Uredo mimica sp. nov.

Uredia hypophylla, subepidermalia, sparsa vel laxe aggregata, bullata, flavida, 0.1–0.2 mm. diam.; urediosporae ellipsoideae vel late ellipsoideae,  $13–16\times17–20\,\mu$ ; membrana 1–1.5  $\mu$  cr. hyalina vel pallide flavida, echinulata, poris germ. obscuris.

On Microglossa volubilis (Wall.) DC., Wareo, Dec. 26, 1936 (1373a, type); Yunzaing, June 11, 1936 (ex 3277A).

Uredo mimica is close to Uredo Microglossae Petch but has decidedly smaller and more nearly globoid spores. The two species were both present in the last number cited.

#### Aecidium foederatum sp. nov.

Pycnia amphigena, subcuticularia,  $115-170~\mu$  diam., hemisphaerica vel conica, maculis flavidis incrassatulis usque 5 mm. diam. occupantibus. Aecia epiphylla inter pycnia sparsa, peridio destituta, profunde immersa,  $160-250~\mu$  diam.; aeciosporae irregulariter obovatae, ellipsoideae vel oblongae, utrinque rotundatae, obtusae vel attenuatae,  $17-29 \times 29-45~\mu$ ; membrana hyalina vel pallide flavida, irregulariter  $1.5-3.5~\mu$  cr., ad apicem et basim  $3-10~\mu$ , remoteque verrucoso-echinulata.

On Glochidion sp., vicinity of Samanzing, Dec. 9, 11, 1938 (10344), Dec. 11, 1938 (s. n.), Jan. 7, 1939 (s. n., type).

Accidium foederatum has the same structure as A. innatum Sydow & Butl. and the aecia of Crossopsora Sawadae (Sydow) Arth. & Cumm. and C. Clemensiae Cumm. but is readily distinguishable because of its larger irregular spores with the wall much thickened apically and basally. The sculpture of the walls is of the same nature as in C. Sawadae and C. Clemensiae but more remote or perhaps absent in some spores. Aecidium innatum is described as having densely verrucose aeciospores. A peridium is lacking in all but the sorus is aecidioid in shape.

## AECIDIUM KAERNBACHII P. Henn.

On *Ipomoea Pes-caprae* (L.) Roth, Lae, July 15, 1939 (10449). On *Ipomoea* sp., Malalo Mission, Salamaua, Aug. 20, 1935 (6); Lae, July 15, 1939 (10450bis). On *Merremia* sp., Malalo Mission, Salamaua, Aug. 22, 1935 (10); Sattelberg, Sept. 28, 1935 (272), Feb. 15, 1936 (1844); Lae, July 15, 1939 (s. n.).

Following studies conducted in the Philippine Islands Stevens and Mendiola (Phil. Agric. 20: 7. 1931) transferred this species

to the genus *Endophyllum*. Since they also found that spores from apparently the same rust on *Lepistemon obscurum* produced "long indeterminate infection tubes" and since their illustrations are not too convincing it seems best to list this species under *Aecidium*.

#### Aecidium advectitium sp. nov.

Pycnia hypophylla, subepidermica, globosa,  $85-120~\mu$  diam. Aecia hypophylla, plus minusve aequaliter denseque distributa, totam folii superficiem occupantibus, cupulata, brevi, 0.2-0.4~mm. diam.; cellulis peridii globosis vel rhomboideis,  $18-26\times23-30~\mu$ ; pariete interiore  $3~\mu$  cr. rugoso, exteriore  $4-5~\mu$  cr. striato; aeciosporae globosae vel late ellipsoideae,  $20-26\times24-30~\mu$ ; episporio  $1-1.5~\mu$  cr. hyalino, verruculoso.

On *Plantago* sp., Mt. Sarawaket, June 15, 1939 (s. n.); Upper Camp A, Mar. 11, 1939 (10009, type).

This species differs from A. Plantaginis-variae McAlpine because of its systemic habit, but seems to be similar otherwise.

#### AECIDIUM MICROSTOMUM Berk.

On *Pratia angulata* Hook. f., vicinity of Samanzing, Nov. 22–23, 1938 (9359), Dec. 9 and 22, 1938 (s. n.); Marsh Meadow Camp, Feb. 10, 1939 (s. n.).

All of the specimens are rather fragmentary but the rust is probably this species, which has systemic aecia without peridia or with only scattered perial cells present. Pycnia were not found, although they have been described for the species.

# Aecidium Hecatactidis sp. nov.

Pycniis non visis. Aeciis amphigenis, cupulatis vel breviter cylindraceis, 200–250  $\mu$  diam., totam folii superficiem occupantibus; cellulis peridii firme conjunctis, rhomboideis, ellipsoideis vel oblongis, 15–18  $\times$  23–35  $\mu$ , pariete interiore 2.5–3  $\mu$  cr. rugoso, exteriore 3–4  $\mu$  cr. striato; aeciosporae globoideae vel late ellipsoideae, 12–16  $\times$  15–19  $\mu$ ; membrana 1  $\mu$  cr., hyalina, minuteque verruculosa.

On *Hecatactis* sp., Upper Camp, Feb. 15, 1939 (9841bis, type); Mt. Sarawaket, June 8, 1939 (s. n.).

THE ARTHUR HERBARIUM,
PURDUE UNIVERSITY AGRICULTURAL EXPERIMENT STATION

# NOTES ON THE MYCETOZOA-IV

#### ROBERT HAGELSTEIN

The fruiting bodies of the Mycetozoa did not appear abundantly during the summer of 1939 in the territory that we usually cover. The lack of early spring rains, so necessary to the revival of the sclerotium, and the long drought which did not end until the middle of August, made collecting almost useless until then.

Mr. Rispaud and I attended the Foray of the Mycological Society of America held in the Great Smoky Mountains National Park, August 17–20. We arrived two days earlier and found that it had been dry for several weeks, so that no developments were seen except old ones which appeared after the preceding rains. During and following fresh rains, the conditions became better, and we stayed long enough to take advantage of them. Our best location was the series of small ravines crossing the road a few miles south of Newfound Gap, at an altitude of about 4000 feet, although good forms were found elsewhere. Didymium crustaceum Fries was coming out at almost every stopping place and was probably the most abundant species fruiting at the time. It matures well under ordinary travelling facilities provided the outer shell has formed. Physarum Listeri Macbr. and Trichia erecta Rex were not rare in the pine and hemlock belts at 4000 feet, and four or five collections of each were made. These species were also abundant in the Laurentian Mountains of upper Quebec after last year's Foray. Two groves of bearing chestnut, old trees that survived the blight, were located in North Carolina and Virginia at 3000 feet or more. The fallen burs from the preceding year had numerous colonies of Arcyria globosa Schw. A development of Comatricha subcaespitosa Peck was eight feet across, but this species often forms large colonies. Physarum sulphureum Alb. & Schw., and its variety sessile, were taken several times, and their occurrence in association confirmed the opinions expressed in my Notes of last year describing their abundance in Quebec. In addition to the species more critically discussed in the later notes of this paper, there were also found Cribraria elegans Berk. & Curt., Diachea bulbillosa (Berk. & Br.) List., Physarum citrinellum Peck, Trichia subfusca Rex, and many of the more common ones. The region, with its divers typographical features, timber belts of many kinds, and heavy annual rainfall, is ideal territory for the Mycetozoa, perhaps the best in the eastern United States.

Dr. Roy F. Cain spent some time collecting in Algonquin Park, Ontario, during the summer, and found among many others the rarely collected species *Badhamia decipiens* (Curt.) Berk., *Cribraria purpurea* Schrad., and *Diachea subsessilis* Peck. These forms may be common enough in other areas, but have seldom been seen in our journeys.

Wood with specimens that has been thoroughly dried in preparation for the herbarium becomes so hard at times that it is difficult to cut and trim with an ordinary knife. The best tool for this purpose is the old style razor still used in barber shops. Ask your barber to save for you the discarded ones that are useless for shaving. They should be taken out of the handles by driving out the pins that hold them, and mounted in an ordinary tool handle with supporting wedges to keep them tight. They need no further sharpening, and when nicked too much by frequent use are thrown away.

The ordinary forceps used for picking off sporangia intended for observation by the microscope are usually too coarse for manipulating the smaller ones. They can be ground to finer points on a stone, but this requires experience or the points may not match. A better way is to buy from a dealer in watchmaker's supplies the forceps used in picking up minute screws and other small parts of watches. These are ground to fine, matched points and are worth the investment.

In the following notes the year 1939 is meant when no other year is given, and the collections were made by Mr. J. H. Rispaud and me, in company, unless otherwise indicated.

BADHAMIA OVISPORA Racib. Reported again by E. Davis and W. D. Sutton as found at Byron, Ontario, in May. N. Y. B. G. Nos. 8980, 9173.

CALONEMA AUREUM Morg. Two fine examples of the form were found during our trip to the Great Smoky Mountains in

August, one in North Carolina, and the other in Virginia. In both the faint spirals on the threads of the netted capillitium wind like a left-handed screw as in *Oligonema nitens* (Lib.) Rost. or in *Trichia*. The spores are reticulated like the spores of *Oligonema flavidum* Peck. The same features are in other specimens of the species here.

Developments of the common *Oligonema* should never be passed in the field but taken and the capillitium examined in order to find the rare *C. aureum*. In *Oligonema* this consists of free elaters. In *Calonema* it is a network. They are practically indistinguishable in the field, even with a hand lens. Our specimens were found by making a special drive, knowing the species occurred in the region, and taking every insignificant *Oligonema* back with us. The netted capillitium was not noticed until after our arrival home. N. Y. B. G. Nos. 2963, 2964.

COMATRICHA RISPAUDII Hagelstein. The species was found again by Mr. Lloyd G. Carr in Augusta County, Virginia, in July. Besides the type locality on Long Island, New York, it has heretofore been collected at Ithaca, New York, and Hanover, New Hampshire. N. Y. B. G. No. 9266.

Comatricha Suksdorfii Ellis & Ev. Collected by J. H. Faull on leaves of the balsam-fir at Lake Timagami, Ontario, in June 1937, and communicated by Roy F. Cain. The sporangia are small and globose, much like those collected by Sturgis in Colorado (Colo. Coll. Pub. Sc. Ser. 12: 33. 1907). The spores are 9–13  $\mu$  diam., purplish-gray, but more strongly spinulose than those in specimens from Oregon and Washington. N. Y. B. G. No. 8330.

Cribraria Laxa Hagelstein. The species has been found here-tofore only in a limited area of a few hundred square feet at Albertson, Long Island, New York. It is gratifying, therefore, to note its collection in Augusta County, Virginia, by Mr. Lloyd G. Carr in July. The development is typical in every respect, even to the habitat on ground leaves and sticks. N. Y. B. G. No. 9262.

Cribraria splendens (Schrad.) Pers. The species is not common although we have found it before in Maine and in Central New York. A small but perfect colony was collected on the

summit of Klingmans Dome, Sevier County, Tennessee, at an altitude of 6600 feet, in August. The form resembles superficially the common *Cribraria intricata* Schrad. var. *dictydioides*, and small colonies which appear like the latter should not be ignored too hastily. N. Y. B. G. Nos. 3087, 3595, 4995.

DIACHEA CYLINDRICA Bilgr. The species, so far as I know, has only been reported from Pennsylvania and New Hampshire. It was found again by Dr. H. C. Beardslee at Longwood, Florida, in December 1938. The form was regarded as a *Comatricha* by Macbride, but in the latter genus the stalk and columella are solid like in *Stemonitis*. In *Diachea* they are tubular, usually filled with lime granules, occasionally with lime crystals, or rarely without lime. In *D. cylindrica* the columella is tubular although lime-less. In this species—admittedly perplexing—it seems to me that the tubular columella is the important generic character. N. Y. B. G. No. 8955.

DIANEMA HARVEYI Rex. This rare species which has not been reported from North America in many years, and then only twice, was found again by Eli Davis at Komoka, Ontario, in October. The all important character is the capillitium which consists of plain, simple threads divided into a few strands at the tops, and running from the base to the upper part of the sporangium-wall. The threads are not ornamented with spirals like in *Prototrichia metallica* (Berk.) Massee which the form resembles in general appearance. N. Y. B. G. No. 9178.

DIDERMA MONTANUM Meylan. A collection of var. album (Torrend) List., on leaves, was made by Eli Davis at Komoka, Ontario, in October 1938. The sporangia are subglobose, not umbilicate, on stout stalks, with a prominent columella which may be a rounded extension of the stalk or somewhat spherical. All are white throughout due to the density of the globose, white, lime granules. The capillitium has colorless, slender threads, and slightly flexuose; the spores are pale purplish-brown, minutely spinulose, and measure  $8-10~\mu$  diam. The spores are not like those of Diderma radiatum (L.) Morg. which are dark and usually larger.

Superficially, this form resembles smooth phases of *Didymium* squamulosum (Alb. & Schw.) Fries, and students are cautioned

to examine carefully all gatherings of the latter species, as the two may be confused if the generic character is overlooked.

During the same month, at the same locality, Mr. Davis also made a small collection of what may be the typical *D. montanum*. The sporangia have the separable inner wall which is lacking in the other collection, but other features are not there, and they bear the same perplexing relationship to *D. radiatum* var. *umbilicatum* which I noted in discussing similar forms from Long Island, New York (Mycologia 28: 584–585. 1936). Further collections of the species and variety are needed in order to obtain a better understanding of their relations to *D. radiatum*. N. Y. B. G. Nos. 9179, 9180.

DIDERMA RUGOSUM (Rex) Machr. A few typical sporangia on a leaf were found near Gatlinburg, Tennessee, in August, during the Foray of the Mycological Society of America. The form may be mistaken in the field for a poorly developed *Didymium nigripes* (Link) Fries. The fruiting period for the locality is probably about the first of August. N. Y. B. G. No. 4998.

DIDYMIUM COMPLANATUM (Batsch) Rost. The form resembles plasmodiocarpous phases of *Didymium squamulosum* (Alb. & Schw.) Fries, so that similar specimens should not be rejected until carefully examined with the microscope.

It was found by Dr. Erdman West at Gainesville, Florida, in July 1935. The capillitium has the numerous, large vescicles, warted like the spores, which are characteristic of the species. Otherwise there is nothing to distinguish it from similar plasmodiocarps of *D. squamulosum* which we have collected. N. Y. B. G. No. 6872.

DIDYMIUM OCHROIDEUM G. List. Found by Eli Davis at Byron, Ontario, in May. The color is somewhat paler than usual, and the spores are a little larger,  $8.5-9.5~\mu$  diam., in these respects similar to a specimen from Long Island, New York, where the species has been found on several occasions and varying slightly in characters. N. Y. B. G. No. 8989.

Fuligo megaspora Sturg. A specimen in the Herbarium of the New York Botanical Garden collected by the Rev. J. M. Bates at Long Pine, Nebraska, in July 1896, and labelled *Spumaria alba* is the present species. The lime is in large spherical granules.

The spores are 20  $\mu$ , or more, diam., very dark, and warted. Two collections from Dr. Erdman West made near Gainesville, Florida, in August 1933 and October 1935 are also the same species and are similar except that the spores are smaller, 12–15  $\mu$  diam. N. Y. B. G. Nos. 5185, 5770, 7136.

HEMITRICHIA INTORTA List. This rare species was found by Eli Davis at Komoka, Ontario, in April. The specimen is finely developed and practically the same as the one from Massachusetts described in Mycologia 30: 347–348, 1938. N. Y. B. G. No. 9181.

LACHNOBOLUS CONGESTUS (Somm.) List. Not common in North America. It forms small clusters of heaped sporangia 3 to 8 mm. across and inconspicuous, so that it may be mistaken in the field for *Oligonema nitens* (Lib.) Rost. which it resembles. The capillitium and spores are diagnostic. Collected by W. D. Sutton at Komoka, Ontario, in December 1938. N. Y. B. G. No. 8978.

LICEA BIFORIS Morg. The size of the sporangia is usually given as not exceeding 0.2 mm. In a specimen received from the Great Khingan Mountains of upper Manchuria there are many that measure 0.4 mm. with some that are 0.5 mm. Collected August 1931. Some authors still adhere to the position that differences in size warrant the proposal of new species. I cannot agree with them. There must be other and more important characters. N. Y. B. G. No. 8647.

LICEA MINIMA Fries. An unusual phase of this species was found by Travis E. Brooks in Geary County, Kansas, in March 1938. The sporangia are extremely small, 0.1 mm. diam. or less, of a chestnut-brown color, and angular with the usual lines of dehiscence. They resemble *Licea castanea* G. List., but the spores are lilac in color and measure  $10-12\,\mu$  diam. The usual phase of the species, which is common on dead coniferous wood, has much larger sporangia, almost black in color, and the spores are olivaceous-brown. N. Y. B. G. No. 9193.

Lycogala epidendrum (L.) Fries. Heretofore I have always regarded small, dark phases of this species as Lycogala exiguum Morg. Occasionally we have found large forms that are very dark, or small ones that are very pale, and these could not be placed satisfactorily. I have made a careful study of all specimens

of L. epidendrum in the Herbarium of the New York Botanical Garden, and have come to the conclusion that L. exiguum must be regarded as a variety of L. epidendrum as Lister accepted it, and not as a valid species. The fact is, when I remove from what was formerly regarded as L. exiguum the forms that are clearly var. tessellatum—the second variety recognized by Lister—there is nothing left to distinguish the others except size, as the color may be dark or pale, and in all other respects they are the same as the typical form. Mere size or color are not sufficient to maintain a species, particularly here, as L. epidendrum in the typical phase varies in the size of the aethalia from very small to very large in the same colony, and also varies considerably in color in different developments. There is no important character to separate the various forms except the superficial vesicles in the cortex later described.

There are 33 specimens here which come within the range of the two varieties mentioned. Of these, 18 are var. tessellatum and very dark in color, due mainly to the multitude of vesicles in the walls of the aethalia. In all but two, the aethalia range in size from 1.2 mm, to 5 mm. The odd two are 7 mm, to 8 mm. well within the range of typical L. epidendrum. When the aethalia are examined with sufficient magnification as opaque objects, the vesicles are seen as irregular protuberances or warts, or thinly spread over small areas and so close together that they appear continuous. In most of the specimens the vesicles are densely pitted with minute depressions, but in two or three they are not so conspicuous. I have not observed this pitting in aethalia of typical L. epidendrum or in var. exiguum. If now a portion of the wall of an aethalium is observed through the microscope with transmitted light, it will be seen that the red vesicles are divided by partitions into many conspicuous, polygonal chambers, giving a celllike or honeycomb appearance. These are usually in one layer but occasionally in more. The chambers are not found in the vesicles of typical L. epidendrum or var. exiguum. This is a character that distinctly sets out var. tessellatum.

The remaining 15 specimens are regarded here as var. exiguum. The aethalia range in size from 1.2 mm. to 3 mm., and in the majority are dark as in var. tessellatum with some reddish or pale

ochraceous. The color is influenced somewhat by the number of vesicles and their thickness. These cannot be regarded as more than a variety.

Morgan in describing *L. exiguum* (Jour. Cin. Soc. Nat. Hist. 15: 134. 1893) did not mention chambered vesicles, and the description fits superficially forms of both varieties as here recognized. It is possible that he had both among his herbarium material, but even so, this cannot invalidate the later name proposed by Lister as var. *tessellatum* (in Penz. Myx. Buit. 77. 1898) for the form with chambered vesicles.

Specimens of var. tessellatum in the New York Botanical Garden Herbarium are from New York, Pennsylvania, Virginia, and Florida. Var. exiguum is there from New York, Pennsylvania, West Virginia, North Carolina, Tennessee, Quebec, Austria, Roumania, and Switzerland.

Material distributed as Lycogala exiguum Morg, should be checked. Likewise, specimens that I have determined under that name.

Physarum aeneum R. E. Fries. A specimen was found near Pulaski, Wythe County, Virginia, in August, by Robert H. Rispaud, the nine year old son of Mr. Joseph H. Rispaud who accompanies his father on many trips, and has been successful in finding many small forms. The collection consists of a few sporangia and plasmodiocarps on a single leaf. The lime in the capillitium is much paler than usual. N. Y. B. G. No. 4997.

Physarum albescens Machr. A fine collection, on plant stems, was made by J. W. Thomson in Juneau County, Wisconsin, in August 1937. The sporangia are sessile, pale in color, and with few traces of the usual hypothallus. The numerous, large, branching lime-knots in the capillitium are pale yellow, almost white. The spores are purplish-brown, not dark, spinulose, and measure  $10-12 \mu$  diam. N. Y. B. G. No. 8970.

Physarum bogoriense Racib. We have found this species repeatedly in New York, Pennsylvania, Virginia, North Carolina, and Quebec, so it is well distributed in eastern North America. Colonies here are small, not like the large ones found in the tropics, and the dehiscence into reflexed lobes is not so conspicuous. It is often associated with *Physarum bivalve* Pers., and distinguished

therefrom by the yellow or brown color and the rounded plasmodiocarps on narrow bases. The spores are usually paler and smaller than those of *P. bivalve*. From *Physarum aeneum* R. E. Fries it is separated by the white lime in the capillitium which is yellow or brown in *P. aeneum*. Many specimens in the Herbarium of the New York Botanical Garden.

PHYSARUM LEUCOPUS Link. The species is rather common. We have found it frequently in the past, and during the season of 1939 in Swain County, North Carolina, Wythe County, Virginia, and Long Island, New York. It forms small colonies and is often associated with Didymium squamulosum (Alb. & Schw.) Fries which it resembles to the unaided eve. It should be searched for in old leaf piles where leaf species are fruiting in abundance. Our practice when such are found is to take all leaves with sporangia. and without examination place them into a box, to be sorted out after our return. By this we save time in the field and occasionally find something worth while in the box which might have been overlooked otherwise. The stalk of P. leucopus is usually furrowed, white, short, stout, and tapering. It may be at times longer, thinner, of equal thickness, or yellowish. The circular hypothallus may be absent. The main characters which distinguish it from Physarum globuliferum (Bull.) Pers. are the loose, lax capillitium and the absence of a defined columella. Many specimens in the Herbarium of the New York Botanical Garden

Physarum megalosporum Machr. The form was first described by Sturgis (Mycologia 9: 323–324. 1917) as Physarum melanospermum. The latter name was used by Persoon (in Roemer N. Mag. Bot. 88. 1794) for what is now known as Didymium melanospermum (Pers.) Machr. so that it cannot be used again and must be superseded by Machride's name. The species has been found, apparently, heretofore only in Colorado by Bethel or Sturgis. It is refreshing, therefore, to note its collection again, this time in Geary County, Kansas, by Travis E. Brooks in August 1938. The development is typical with flattened, centrally depressed sporangia on stout, black stalks, and very dark spores  $12-13 \mu$  diam. having a paler area. Some of the stalks are yellowish, and some of the sporangia subglobose or bolster-shaped, but not sessile.

Macbride, in the North American Slime-moulds, and Macbride and Martin in the Myxomycetes describe and key the species as primarily sessile. This is not so and creates confusion as to what the species really is and also doubts as to whether it is the same as *P. melanospermum*, because Sturgis described his species as a stalked one. The specimens of Sturgis are in the Herbarium of the New York Botanical Garden and show clearly that the species forms stipitate sporangia primarily, and while it cannot be denied that there may be sessile sporangia in some other collection, this would be of secondary importance. N. Y. B. G. No. 9191.

Physarum superbum nom. nov. The name is proposed for the form represented by figures a (Philadelphia) on plate 22 in the second and third editions of the Lister Monograph. In the second edition it was regarded as *Physarum variabile* Rex var. sessile, and in the third, as *Physarum sessile* Brandza.

Brandza (Ann. Sc. de l'Univ. Jassy 11: 116-117. 1921) proposed the name Physarum sessile to cover two forms in Roumania. a white one and a yellow one, including therewith P. variabile var. sessile. Later (Bull. Soc. Myc. Fr. 44: 260-262. 1929), he separated the white one as P. sessile, and proposed Physarum aureum for the yellow one. The white form was distributed by Brandza in exsiccatae in 1920 as P. variabile var. sessile, and again in 1922 as P. sessile. These specimens are here and consist of white cylindrical plasmodiocarps and globose sporangia with pale, smooth spores 7–8  $\mu$  diam. They are closely related to *Physarum cinereum* (Batsch) Pers., and probably only phases thereof. Whether or not the yellow form, later named P. aureum, is the same as the one under discussion here is immaterial as Brandza's name cannot be used. Physarum aureum (Pers. in Roemer N. Mag. Bot. 88. 1794) is already in use for a form now regarded as synonymous with Physarum viride (Bull.) Pers.

There is in the former collection of Dr. W. C. Sturgis, now in the Herbarium of the New York Botanical Garden, a specimen collected by the late Hugo Bilgram at Philadelphia in August–September 1900 which is probably a part of the same material used by Lister for his figures a on plate 22. The specimen is accompanied by a letter from Mr. Lister to Dr. Sturgis dated February 3, 1901, in which he mentions interesting specimens received from

Mr. Bilgram, and that he had been drawing them all. He refers to a letter he sent to Mr. Bilgram, a copy of which letter dated February 2, 1901, also accompanies the specimen. This letter comments on various specimens received, including one which he names *Physarum variabile* var. sessile and which is clearly reconciled with the specimen in the former collection of Sturgis. There are also in the Herbarium of the New York Botanical Garden seven other collections made personally on Long Island, New York, and in the Great Smoky Mountains region of North Carolina and Tennessee, and another from North Carolina found by the late Prof. R. Thaxter. All are identical with the Philadelphia collection of Bilgram and figures a on plate 22 of Lister, except that two are neither well developed nor normal.

The fructification, on leaves, is plasmodiocarpous with abbreviated plasmodiocarps down to sporangial size. The plasmodiocarps are annular, sinuose, netted, branched, or straight up to 12 mm. in length or more. The color is yellow to orange-red. The plasmodiocarps are not cylindrical in cross-section, but more or less laterally compressed and on broad bases. The sporangium-wall has heavy deposits of yellow or orange-yellow lime granules, often unevenly distributed, or scanty in the lower part, presenting a mottled appearance. The lime-knots in the capillitium are abundant, angular, irregular or branching, white or pale yellow, sometimes densely aggregated in the center. The spores are somewhat pale brownish-lilac, minutely and evenly spinulose,  $7-8.5~\mu$  diam. The characters are remarkably uniform throughout the collections.

These plasmodiocarps cannot be associated with P. variabile (or Physarum sulphureum Alb. & Schw. as now regarded) because of the habit, color, and smaller spores. There are sessile sporangia and plasmodiocarps of P. sulphureum (Mycologia 31: 346–348. 1939) which are like figure b on Lister's plate 22, and have larger spores. They are not P. sessile Brandza, obviously, an entirely different form. I doubt that P. aureum Brandza belongs with them as it is described with spores  $10-12 \mu$  diam., and figured with cylindrical plasmodiocarps. The beautiful form on Lister's plate 22 as figure a requires a name that is appropriate and tenable. I propose for it, Physarum superbum.

Material distributed from here under one of the various names

mentioned should be corrected. N. Y. B. G. Nos. 786, 1253, 4973, 4974, 4979, 4989, 4990, 11027, 11550.

PROTOTRICHIA METALLICA (Berk.) Massee. Rarely, if ever, reported from the eastern United States, although not uncommon in the West. It was found in August near Newfound Gap, Swain County, North Carolina, at an altitude of 4200 feet. The sporangia are much like those of *Margarita metallica* (Berk. & Br.) List. or *Dianema Harveyi* Rex, but the capillitium is different, consisting of threads wound with prominent spirals and divided at the tops into bundles of thinner threads, with attachments to the peridium at both ends. N. Y. B. G. No. 2933.

THE NEW YORK BOTANICAL GARDEN

# CONTRIBUTIONS TO THE MYCOFLORA OF BERMUDA—I

F. J. SEAVER AND J. M. WATERSTON

(WITH 6 FIGURES)

During the late autumn of 1938 (November 28 to December 14) the senior author made a third visit to Bermuda in continuation of the mycological survey of the islands, initiated by The New York Botanical Garden more than a quarter of a century ago, and continued intermittently to the present time.

The first expedition, in connection with the above work, was made in the year 1912, covering almost exactly the same seasonal dates as our recent one. Thus the third visit represented a twentysixth anniversary of the first. At the time of the first visit scarcely more than a score of fungi were known from the islands, and the place had the reputation of being almost barren of this particular form of plant life. Consequently the voyage was undertaken with some misgivings. These fears, however, proved to be groundless for as a result of this first short visit, the number of known species of fungi was increased to considerably more than a hundred, a list of which was published in the Memoirs of The New York Botanical Garden in August, 1916, and constituted the first extensive list published of the fungi of the islands. A few new species were included. The results of the second expedition, in company with Professor H. H. Whetzel, are left out of consideration since most of the material collected on this occasion (1926) is in Cornell University, and for the most part unworked.

The remoteness of these islands, together with the fact that they have apparently never been connected with any other existing body of land, adds interest to the study of their land flora. Although the fungi cannot be said to be abundant, on critical study one is impressed first by the number of species found there which are not known to occur in other parts of the world, although we do not usually think of the fungi as being restricted to very limited

areas, and second by the number of species occurring abundantly in Bermuda which are known but rarely in other parts of the world. The fungi seem to defy all known rules of distribution, and follow a course of their own. Some of the idiosyncracies in the distribution of the fungi will be discussed in the present paper. In doing this we will first consider two European species which were reported from Bermuda on our first visit, and which on our late return were re-collected and found to be thoroughly established, and in one case exceedingly abundant but concerning which little is known in Europe and nothing at all on the mainland of North America.

#### EUROPEAN SPECIES

Lamprospora Planchonis (Dun.) Seaver. This species was originally described from material collected in France and published in 1887. We have seen no further mention of the fungus from Europe, but in 1912 it was found to be very common in Bermuda. In 1914 Dr. R. Maire collected the species in North Africa and distributed it under the name *Plicaria Planchonis* (Dun.) Boud. in his Mycotheca Boreali-Africana no. 192. In Bermuda this fungus is ubiquitous and so abundant on sandy soil and sand dunes that one finds himself wondering why nature could not have made more different kinds of cup-fungi there instead of making so many of the same kind, forgetting for the time that we were collecting a fungus that was rare in Europe and entirely unknown in the New World unless Bermuda be regarded as part of the New World.

There has always been some confusion between this species and Ascobolus Persoonii Crouan, and Saccardo intimates that the two may be the same fungus. If so, this might partly account for its apparent rarity in Europe, but still does not explain the fact that it has never been found on the mainland of North America, although the cup which reaches a diameter of nearly two centimeters could not be easily overlooked by students of the group if it occurred here, and certainly not if it were anywhere as abundant as it is in Bermuda. Since these islands have grown up in midocean, it is difficult to account for these peculiarities in the distribution of certain species.

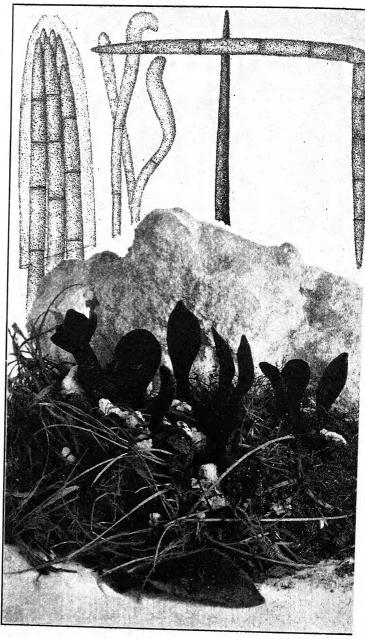


Fig. 1. Trichoglossum Wrightii.

Pseudopithyella minuscula (Boud. & Torrend) Seaver (Fig. 6). This species was described under the name Sarcoscypha minuscula Boud. & Torrend, from material collected in Portugal on the dead foliage of cedar. It was published in 1911, just one year before the senior author collected it on dead foliage of the endemic cedar, Juniperus bermudiana L., in Bermuda. Although no further mention of the species has been noted in Europe, on our recent visit to Bermuda the species was again collected and, while apparently common and thoroughly established, it is not as abundant as the preceding form, and less conspicuous because of its small size.

In the senior author's North American Cup-fungi this was made the type of a new genus characterized by having a protruding ring surrounding the ascus near the tip, a character which has never been observed in any other species of cup-fungi studied. While minute in size the fungus partly overcomes this handicap by assuming a bright scarlet color. The generic name is suggested by its resemblance to *Pithya*, with which it is often associated and which it outwardly resembles, except in color.

Here again we have a rare European species well established and common in Bermuda, but not known from any other part of the world. We might assume from these illustrations that possibly Bermuda had at some remote time been connected with Europe if we did not know better, and were it not for the fact that we have rare North American species which are apparently common in Bermuda but on the other hand unknown in Europe. Two of these will be mentioned as illustrations.

#### NORTH AMERICAN SPECIES

Ophionectria cylindrothecia Seaver (fig. 4, lower). This species was described by the senior author in his monograph of the North American Hypocreales (Mycologia 1:70. 1909). The species has never again been encountered in continental North America and is not known in Europe unless, as sometimes happens, it has been described under some other name. The type species was described from material collected on old stalks of corn, Zea Mays L., in Ohio, exact date not given. In 1922 the senior writer received from H. H. Whetzel, then temporarily located in Berreceived

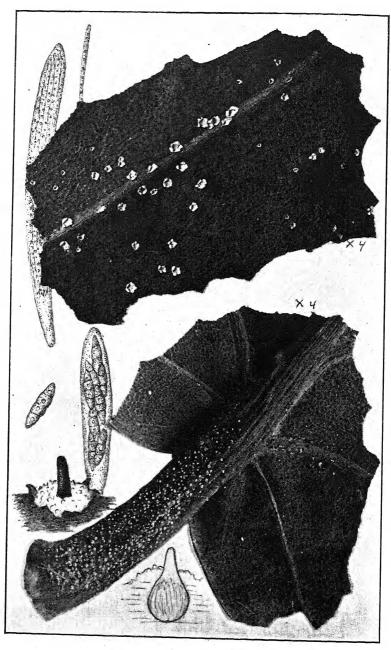


Fig. 2. Stictis Coccolobii.
Gnomonia pulcherrima.

muda, specimens on the petiole of Bermuda palmetto, Sabal bermudana L. H. Bailey, which were at once recognized as his own species named above. During our recent visit the species was again twice collected on the same substratum. Thus a species described more than a quarter of a century ago from continental North America on monocotyledonous stems has been encountered three times on similar substratum in Bermuda, but has never again been found on the mainland. This particular case might be explained by the fact that the fungus is minute and inconspicuous and has escaped notice. But the same explanation will not hold for some other forms.

Torula diversa Cooke (fig. 5). This fungus was described by M. C. Cooke from material collected on the leaves of *Agave* at Darien, Ga., published in Grevillea in 1878, and distributed by H. W. Ravenel in his Fungi Americani Exsiccati no. 283. The fungus forms sooty spots conspicuous enough to be easily seen by anyone interested in the study of parasitic fungi, yet so far as can be discovered this fungus described more than sixty years ago has not been encountered again in continental North America, but was found to be fairly abundant on *Agave* leaves in Bermuda during the past winter. Other examples might be given, but these will serve to illustrate the unique character of the mycoflora of Bermuda.

#### ENDEMIC SPECIES

Because of the ease with which the spores of the fungi may be blown about, we do not usually think of them as being restricted to small areas but nevertheless several species have been described from the islands which must be regarded as endemic until they have been discovered in some other region. Two such species described by the senior writer in 1916 from material collected in 1912 deserve special mention.

NECTRIA LANTANAE Seaver. This species was first found on the under side of fallen leaves of *Lantana odorata* L. After so long a time the writers during the last winter were anxious to know whether the fungus continued to recur on the leaves of this host, or whether it was just a chance infection. A preliminary search revealed nothing and we had almost given up hope of rediscovering

this fungus when on December 8, while collecting on St. David's Island, the senior writer casually picked up a handful of fallen Lantana leaves and found several of them dotted over with the red perithecia of the desired Nectria which proved to be fairly abundant. A later collection was made at Grape Bay, and still later the junior author found it in his own dooryard in Hamilton. Thus after twenty-seven years this little fungus which was first collected near Harrington Sound was located in three other stations. Lantana odorata is a shrub which was introduced into Bermuda from the Bahamas prior to 1800, and is now widely distributed. It is difficult to believe that this fungus occurs persistently on the leaves of this host in Bermuda, and not on the same host in other parts of the world. Yet the fact remains that it has not been found elsewhere and must remain an endemic species until it has been discovered in some other part of the world as it doubtless will be.

Calonectria Umbelliferarum Seaver. Another novelty described by the senior writer in his first report of the fungi of the islands occurred on the stems of fennel, Foeniculum vulgare Gaertn., an introduced herbaceous plant which has escaped from cultivation and become widely disseminated in the islands. As in the preceding case, the fungus was at first looked for without results. Finally, on December 9, it was located in Smith's Parish. Later the junior author sent other specimens on the same host from Somerset, again showing that the fungus was well established on this host in Bermuda, but up to date has not been found on the same host outside of Bermuda. It is not unlikely that if the same diligent search had been made for these two minute fungi on the same hosts outside of Bermuda they might be found. But the fact remains that this has not yet been done.

Scleroderma bermudense Coker. During the second visit to Bermuda the senior author observed the remains of a fairly large *Geaster*-like fungus on the sands of the south shore. Closer observation showed that this puffball matured entirely submerged, first appearing as a crack in the sand. The outer covering of the puffball splits into several star-like rays which roll back and the fruiting body literally lifts itself as by its bootstraps out of the sand. The spore mass is then quickly blown away and all we

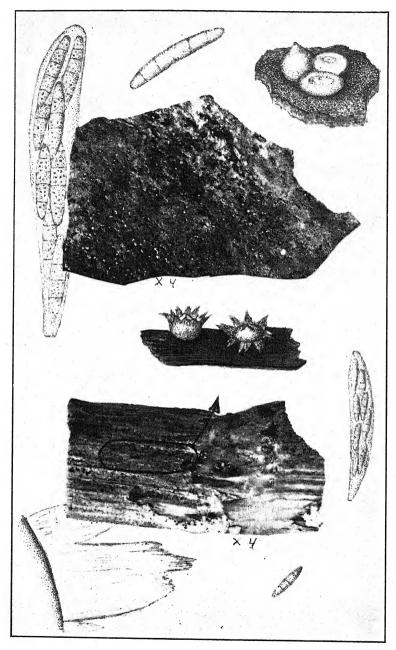


Fig. 3. Calonectria Crescentiae. Calonectria fimbriata.

have left is the outer covering which would appear to the casual observer like a piece of dried leather. It is very difficult to find one of these balls before opening since at that time they are entirely hidden.

On our late visit to the islands a large collection of this peculiar fungus was made near the Elbow Beach Hotel and submitted to Dr. W. C. Coker of the University of North Carolina, an expert in this particular group, for critical study. He pronounced it a new species and described it under the name given above (Mycologia 31: 624. 1939). It is claimed to be the only known Scleroderma which matures entirely under ground. Unlike the two preceding species, this fungus is not too small to be seen by the casual observer. If a palm and a cedar tree could become so modified under conditions of isolation that they come to be regarded as distinct species, why could not the same thing happen to a puffball, as seems to have been the case with this species?

Humarina Waterstonii Seaver. This is one of our most interesting late collections. The species is unusual since it is the only member of the genus encountered which grows exclusively on the seeds of the higher plants. Since the fungus seems to be restricted to the seeds of its host, the Chinese fan-palm *Livistona chinensis* R. Br., it is not unlikely that the fungus might be found where the palm is native. However, no such fungus has been reported and it must be regarded as endemic to Bermuda.

#### ADDITIONS TO THE FLORA

During our recent survey of the islands, a goodly number of species, in addition to those mentioned above, were collected which had not been obtained on our previous excursions, notwithstanding the fact that two of these visits covered exactly the same seasonal dates. This is due in part to the sporadic occurrence of some of the fungi, and in part to the fact that on account of their obscure character it is impossible to find all that occur at any one time. A number of these appear to be new to science. While the collection has not all been studied, we list below new and noteworthy species that have thus far been determined, and it is expected in later papers to publish from time to time additional discoveries.

#### NEW SPECIES

# PEZIZALES (INOPERCULATES)

## Helotium atrosubiculatum sp. nov.

Apothecia thickly gregarious, occasionally forming congested masses, stipitate gradually expanding above becoming shallow cupshaped, occasionally convoluted 2–4 mm. in diameter and about 2 mm. high, externally grayish-brown and pruinose; hymenium concave, whitish even or in larger specimens convoluted; asci clavate reaching a length of 60  $\mu$  and a diameter of 6  $\mu$ ; spores ellipsoid, each containing two oil-drops 2–2.5  $\times$  6–7  $\mu$ ; paraphyses filiform, about 1  $\mu$  in diameter.

Apotheciis gregariis, stipitatis, applanatis, griseis vel brunneis, 2-4 mm. diam., 2 mm. alt.; hymenio concavo, subalbido; ascis clavatis,  $60 \,\mu \times 6 \,\mu$ ; sporis ellipsoideis,  $2-2.5 \times 6-7 \,\mu$ ; paraphysibus filiformibus,  $1 \,\mu$  diam.

On the blackened surface of leaves of Archontophoenix Alexandrae Wendel & Drude, rotting on the ground, 71.

Type collected at Hungry Bay, December 2, 1938. The black subiculum seems to be a constant character in this species. The base of the stem is also black and easily detached near the base leaving disc-like scars which themselves look like minute discomycetes.

# Dasyscypha fasciculata sp. nov.

Apothecia thickly gregarious, occurring singly or more often in dense fasciculate clumps, several apparently springing from the same base and so closely compact that they appear to be one compound fruit body, short-stipitate, externally clothed with a dense covering of white hairs, the clumps scarcely exceeding 1 mm. in diameter, the individual apothecia much less; hymenium concave, pale-orange; hairs flexuous, hyaline, externally roughened, about 2  $\mu$  in diameter; asci clavate, reaching a length of 35–40  $\mu$  and a diameter of 4  $\mu$ , 8-spored; spores minute, fusoid, hyaline, 1.5  $\times$  6  $\mu$ ; paraphyses filiform semi-acute but scarcely lanceolate.

Apotheciis gregariis aut fasciculatis, breve stipitatis, extus pilis albis tectis, vix 1 mm. diam.; hymenio concavo, flavo-aurantio; pilis flexuosis, hyalinis,  $2\,\mu$  diam.; ascis clavatis,  $35-40\,\mu \times 4\,\mu$ ; 8-sporis; sporis fusiformibus hyalinis,  $1.5\times 6\,\mu$ ; paraphysibus filiformibus aut sublanceolatis.

Type collected on rotten stumps of olive tree *Olea europaea* L., 45. Walsingham, Nov. 30, 1938.

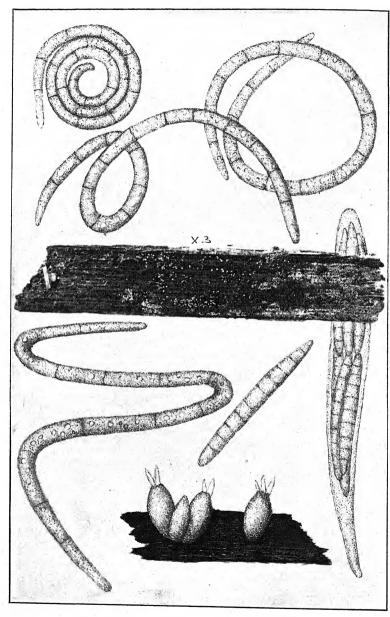


Fig. 4. Helicomyces roseus.

Ophionectria cylindrothecia.

## Gorgoniceps confluens sp. nov.

Apothecia gregarious, occasionally crowded and several fusing together, sessile or contracted into a very short stem-like base, whitish or bluish-white, remaining light-colored or becoming darker when dried, reaching a diameter of .5 mm. soft and waxy; hymenium plane or slightly convex, similar in color to the outside of the apothecium; asci broad-clavate, with a very short stem-like base, attenuated at the apex, reaching a length of  $100~\mu$  and a diameter of  $14~\mu$ , 8-spored; spores bunched together and overlapping, cylindric, fusoid or subclavate, straight or more often curved or double curved, becoming 7-septate,  $5-7 \times 40-45~\mu$ ; paraphyses filiform, about  $2~\mu$  in diameter.

Apotheciis gregariis, sessilis aut subsessilis, albidis aut subcaeruleis, .5 mm. diam.; hymenio plano vel convexo; ascis late clavatis, substipitatis,  $100 \,\mu \times 14 \,\mu$ , 8-sporis; sporis cylindraceis aut subclavatis, rectis aut flexuosis, 7-septatis 5–7 × 40–45  $\mu$ ; paraphysibus filiformibus 2  $\mu$  diam.

On rotten wood and on palm stems.

Type collected in Bermuda by Stewardson Brown, N. L. Britton and Fred J. Seaver (No. 1487) Nov. 29–Dec. 14, 1929. This is very similar to *G. iowensis* Rehm which was described from material collected by the author in Iowa. The spores of the Bermuda specimens seem to be larger. Also collected in Paget Marsh on stems of native palmetto, *Sabal bermudana* L. H. Bailey 62.

#### PHACIDIALES

#### STICTIDACEAE

Stictis Coccolobii sp. nov. (FIG. 2, upper)

Apothecia on either side of the leaf at first immersed, the epidermis finally rolling back in about five stellate lobes which are white on the inside; hymenium freely exposed at maturity not deeply immersed, whitish or with a slightly olive tint, reaching a diameter of about .5–.75 mm.; asci clavate, 8-spored, reaching a length of  $80 \mu$  and a diameter of  $8 \mu$ ; spores filiform reaching a length of 70– $75 \mu$  and a diameter of  $2 \mu$ , becoming many-septate; paraphyses filiform slender.

Subgregarium, innatum dein epidermide in lacinias 5 vel plures aequales acutas fissa erumpens; hymenio albido vel leniter olivaceo, .5–.75 mm. diam.; ascis clavatis 8-sporis,  $80 \,\mu \times 8 \,\mu$ ; sporis filiformibus, 70–.75  $\mu \times 2 \,\mu$ , multiseptatis; paraphysibus filiformibus.

On leaves of *Coccolobis uvifera* (L.) Jacq. lying on the ground. Type locality: Grape Bay, 13, 196.

The spores of this species are only half as long as those of *Stictis* radiata (L.) Pers., and the apothecia are much more shallow than those of the latter species.

# Stictis lophodermioides sp. nov.

Apothecia thickly gregarious, erumpent, usually elongated, .5 to 1 mm. long and usually one-third as wide, often several coalesced, the ruptured epidermis pallid, whitish within, hymenium yellowish; asci clavate, reaching a length of  $50-60 \mu$  and a diameter of  $8 \mu$ ; spores filiform slender, nearly as long as the ascus.

Apotheciis gregariis, erumpentibus, elongatis, .5–1 mm. long.; hymenio flavo; ascis clavatis, 50–60  $\mu$   $\times$  8  $\mu$ ; sporis filiformibus.

On sheaths of grass (Stenotaphrum?).

Type collected about Harrington Sound by Brown, Britton and Seaver (No. 1469) Nov. 29-Dec. 14, 1912.

This was doubtfully recorded as *Stictis graminum* Desm., but on more careful study was found to differ. In form it suggests a *Lophodermium*, but in other characters it is more like a *Stictis*, hence the name.

#### SPHAERIALES

# Ascospora Citharexyli sp. nov.

Perithecia thickly scattered over both the surfaces of the leaves of the host or occasionally collected in groups, erumpent often becoming semisuperficial subglobose, black; asci clavate reaching a length of 50–60  $\mu$  and a diameter of 12  $\mu$ , 8-spored; spores irregularly 2-seriate, subhyaline, fusoid, strongly swollen in the center with both ends narrowed, usually containing 1 large oil-drop 8  $\times$  16–20  $\mu$ .

Peritheciis sparsis erumpentibus dein semisuperficialis, subglobosis, atris; ascis clavatis, 50–60  $\mu \times$  12  $\mu$ , 8-sporis; sporis subdistichis, subfusiformibus 8  $\times$  16–20  $\mu$  subhyalinis.

On dead leaves of fiddlewood *Citharexylum spinosum* L. Type material collected at Somerset Dec. 17, 1938 by J. M. Waterston 212.

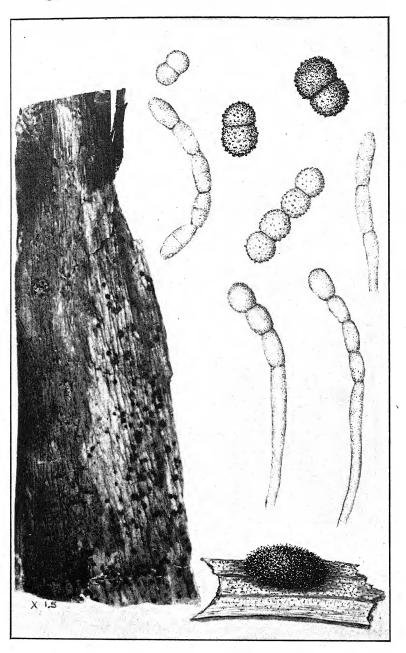


Fig. 5. Torula diversa.

# Gnomonia pulcherrima sp. nov. (FIG. 2, lower)

Perithecia thickly gregarious, entirely buried in the substratum with the long beak protruding, surrounded at the point of exit with a yellowish granular mass consisting largely of angular crystals, the individual perithecia about 250  $\mu$  in diameter, the beak about 400  $\mu$  long and about 80  $\mu$  thick, the walls olive-green in color; asci clavate reaching a length of 50  $\mu$ , and a diameter of 8  $\mu$ ; spores irregularly 2-seriate, fusoid, pale-greenish becoming 1-septate and slightly constricted, containing 3 or 4 oil drops about  $12 \times 4 \ \mu$ .

Peritheciis dense gregariis immersis,  $250 \,\mu$  diam.; ostiolis exsertis  $400 \times 80 \,\mu$  diam., olivaceis; ascis clavatis,  $50 \,\mu \times 8 \,\mu$ ; sporis subdistichis, subfusiformibus olivaceis, uniseptatis,  $12 \,\mu \times 4 \,\mu$ , leviter constrictis.

Type collected on petioles and midribs of leaves of *Coccolobis* uvifera (L.) Jacq. lying on the ground, Hungry Bay 82.

# Penzigia bermudensis J. H. Miller, sp. nov.

Stromata gregaria vel confluentia, subglobosa,  $1-.5\times.5$  mm., apicis convexis vel applanatis, inferne constricta; ectostromatibus atro-brunneis vel nigris, levigatis; entostromatibus suberosa-lignosis albis; peritheceis 1-4 in quoque stromate, globosis,  $300-400~\mu$  in diam.; ostiolis minutis, papillatis; ascis cylindraceis (par. spor.)  $50-70~\mu$  longis, attenuatis stipitis,  $45-65~\mu$  longis; 8-sporis; sporis monostichis, lato-ellipsoideis, apicis obtusis, atro-brunneis,  $8-10\times6-8~\mu$ ; paraphysibus numerosis, ramosis, filiformis. Ad ligna decorticata. 38B. Walsingham, Nov. 30.

This is one of the intermediate species in the Xylariaceae. Macroscopically it resembles somewhat *Rosellinia*, but differs from most species of that genus in possessing a fleshy-leathery outer stromatic crust instead of the carbonous one, and in the white stroma in which the perithecia are embedded. This internal tissue, common in *Xylaria* species, is characteristic of *Penzigia*.

There are other species with few perithecia in the stroma such as *Penzigia frustulosa* (Berk. & Curt.) Mill. and *P. Kellermanii* (Rehm) Mill. in the United States, and *P. conostoma* (Mont.) Mill. in South America. These all differ from the Bermuda fungus in spore dimensions, measuring respectively  $5-6 \times 2.5-3 \mu$ ,  $25 \times 11-14 \mu$ , and  $22-28 \times 8-12 \mu$ .

The Hypoxylon species that have this general appearance are H. confluens (Tode ex Fries) Cooke, and H. udum Fries in Europe, and H. regale Morgan in this country. All of these have much larger spores and all lack the fleshy-leathery white subperithecial stroma.

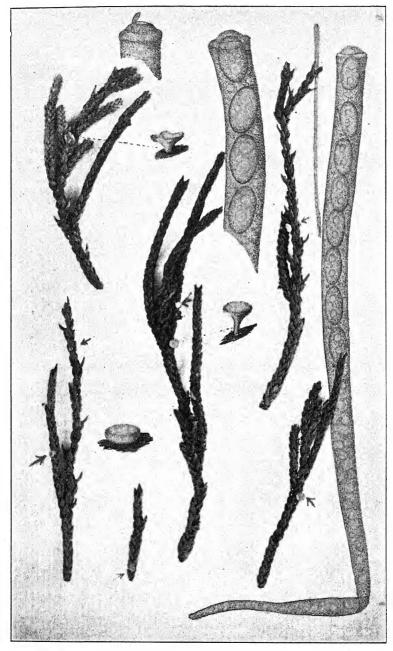


Fig. 6. Pseudopithyella minuscula.

#### HYPOCREALES

# Calonectria Crescentiae sp. nov. (FIG. 3, upper)

Perithecia thickly gregarious or often closely congested but without trace of stroma at first globose, when dried out collapsing and becoming pezizoid resembling in size and form Nectria Pesisa (Tode) Fries; asci clavate, reaching a length of 80  $\mu$  and a diameter of 10  $\mu$ ; spores partially 2-seriate, fusoid slightly curved, variable in size but reaching a length of 30  $\mu$  and a diameter of 6  $\mu$ , granular within, becoming 3-septate and slightly constricted at the septa, hyaline; paraphyses indefinite.

Peritheciis dense gregariis, subsphaeroideis, siccis supra depressis, pezizoideis; ascis clavatis,  $80 \,\mu \times 10 \,\mu$ ; sporis subdistichis, subfusiformibus, curvulis, 3-septatis, leviter constrictis.

Type collected on a weathered shell or fruit rind of the calabash, *Crescentia Cujete* L., in Smith's Parish, Dec. 9, 1938.

# Calonectria fimbriata sp. nov.

Perithecia minute occurring singly or in small congested clusters, pale orange, subglobose collapsing vertically, showing a distinct fringe-like or often stellate margin; asci clavate reaching a length of  $36~\mu$  and a diameter of  $6~\mu$ ; 8-spored; spores irregularly 2-seriate fusoid,  $3 \times 12$ –14  $\mu$  becoming 3-septate, hyaline or subhyaline.

Peritheciis minutis solitariis vel congestis subglobosis dein pezizoideis palidoaurantiis, margine fimbriato vel stellato; ascis clavatis  $6 \times 36 \mu$ , octo-8-sporiis; sporis subdistichis fusoideis, subhyaliniis dein 3-septatis.

On dead stems of Foeniculum vulgare Gaertn.

Distinguished from Calonectria Umbelliferarum Seaver by the minute fringed perithecia and the much smaller spores.

#### NOTEWORTHY SPECIES

#### **BASIDIOMYCETES**

AGARICUS CAMPESTRIS L. The common field mushroom was found well established in a pasture on Kitchener's (Hinson) Island when visited on December 5, 1938. Strange as it may seem, this well known species had not previously been recorded from the islands, and has so far as known up to date been observed only on the one island.

CLAVARIA VERMICULATA Mich. This species was determined by Dr. W. C. Coker as above, with *C. vermicularis* Fries as a syno-

nym. The fungus was first seen on the hillside back of the Hospital Station, Paget East, and is the only *Clavaria* so far reported from Bermuda. It seemed to be rather common during the winter of 1938, having been collected in St. David's Island 149; in Smith's Parish 165, 179; and in Hamilton 189, although it had not been seen on either of the two previous visits, both of which were made during the same season of the year.

Lycogalopsis Solmsii E. Fischer. This small puffball was collected in the Walsingham region on rotten wood on November 30, 1938. It was thought by us to be an immature Lycoperdon, but on study by Dr. W. C. Coker was referred to the above. This species was first described from material collected in Java. One collection has been reported from Honduras, and one from Panama, the Bermuda collection representing the third from this side of the world. It is thought, however, that L. Dussii described from Martinique, and L. subiculosa described by C. G. Lloyd from Porto Rico, are identical with the above. If so, the other two stations should be added to the known distribution of the species. In any case, it is a very rare puffball and its collection in Bermuda represents a wide extension of range.

#### ASCOMYCETES

NECTRIA SUFFULTA Berk. & Curt. This setose *Nectria* was originally described from material collected in Cuba, and has hitherto been known only from the West Indies and Mexico. Its appearance in Bermuda on rotten stumps of wild sisal, *Furcraea macrophylla* Baker, is therefore noteworthy.

LAESTADIA JUNIPERINA (Ellis) Sacc. A fungus on the dying leaves of Bermuda cedar, *Juniperus bermudiana*, appears to be the above species originally described by Ellis from material collected in Iowa on leaves of *Juniperus virginiana*. Ellis also claims that it has been found by Karsten in Finland. It may be responsible for the cedar blight so prevalent in Bermuda during recent years. Field experiment will be necessary to prove this.

TRICHOGLOSSUM WRIGHTII Durand. (FIG. 1.) This was first listed by Durand as a form of *Trichoglossum hirsutum*, based on two specimens from Cuba. Later, on collections of the senior author from Bermuda in 1912 (Britton, Brown & Seaver 1404),

this form was raised to specific rank by Durand (Mycologia 13: 187. 1921). This is one of the commonest species of the genus which is well represented in Bermuda, and was recollected on our recent visit by Mr. T. A. Russell and the senior author 178.

Tryblidella rufula (Spreng.) Sacc. Hawkin's Island was visited and explored on December 5, 1938. One of the noteworthy collections made was the above species which, although common in both tropical and temperate regions, had not previously been recorded from Bermuda. On this occasion it was found to be very abundant on wild *Mimosa* (*Leucaena glauca* (L.) Benth.) 140. Although abundant there it has to date been found only on the one island. It is an interesting coincidence that this fungus has been reported on the same host from the Hawaiian Islands by Miss Cash (Mycologia 30: 101. 1938).

#### FUNGI IMPERFECTI

A number of fungi belonging in the present group have been collected, but most of them determined only as far as the genus. In addition to the one mentioned in the introductory paragraphs of the present paper, one other deserves special mention as follows:

Helicomyces roseus Link. (Fig. 4, upper.) Apparently common in Bermuda, having several times been collected, and always on the stems of the native endemic palm Sabal bermudana L. H. Bailey. The fungus is of especial interest because of its association with Ophionectria cylindrothecia, reported elsewhere in this paper. During the past winter several collections of this ascomycete were obtained. Close examination showed every collection of the ascomycete to be accompanied by the Helicomyces, which was determined by Dr. D. H. Linder as above. Finding the Helicomyces always associated with the Ophionectria in our own collections prompted a re-examination of the Whetzel collection obtained sixteen years before, and it was also found to be accompanied by the same Helicomyces. This again suggested a more careful study of the type material of the Ophionectria collected in Ohio more than thirty years ago (the exact date not recorded), and again the Ophionectria was found to occur with the Helicomyces, but had been overlooked when the fungus was described, or at least not regarded as of any importance. Thus every collection of *Ophionectria cylindrothecia* known is accompanied by the above species of *Helicomyces*, and we predict that the latter will be found to represent the conidial stage of the former. Attempts to germinate the ascospores showed them not to be viable. This connection should be studied from fresh material in the field.

#### NEW TO BERMUDA

In addition to the above mentioned species the following were collected and reported for the first time from Bermuda. This list includes only those for which specific determinations have been made. Much of the material is still in the process of study: Geaster radicans Berk. & Curt.; Lycoperdon Wrightii Berk. & Curt.; Lycogalopsis Solmsii Ed. Fischer; Solenia candida Pers.; Sphaerobolus Carpobolus L.; Ascobolus magnificus Dodge; Ascophanus granulatus (Bull.) Speg.; Orbilia coccinella (Sommerf.) Karst.; Patella melaloma (Alb. & Schw.) Seaver; Patella cubensis (Berk. & Curt.) Seaver; Pezisa vesiculosa Bull.; Diatrypella favacea (Fries) Ces. & DeNot.; Eutypella fraxinicola (Cooke & Peck) Sacc.; Herpotrichia albidostoma (Peck) Sacc.; Hypocrea sulphurea (Schw.) Sacc.; Hypoxylon exutans Cooke; Hypoxylon jecorinum Berk. & Br.; Hypoxylon stygium (Lév.) Sacc.; Megalonectria pseudotrichia (Schw.) Speg. conidia only; Nectria episphaeria (Tode) Fries; Nectria rhytidospora Pat.; Nectria ochroleuca (Schw.) Berk.; Rosellinia aquila (Fries) Ces. & DeNot.; Acrostalagmus cinnabarinus Corda; Monilia aureofulva Cooke & Ellis; Synsporium biguttatum Preuss.

The authors wish to express their appreciation to the Director and other members of the staff of the Bermuda Agricultural Station for their encouragement and coöperation, and to the various mycologists who have assisted in the determination of the material collected. They also wish to thank the officials of the Furness Bermuda Line through whose coöperation this work was made possible.

The New York Botanical Garden and Dept. of Agriculture,
Paget East, Bermuda

# A NEW HOST FOR TAPHRINA DEARNESSII AND GEOGRAPHIC DISTRIBUTION OF TAPHRINA ON NORTH AMERI-CAN MAPLES

Anna E. Jenkins and W. Winfield Ray

(WITH 4 FIGURES)

#### INTRODUCTION

Following the recent emendations of the original description of *Taphrina lethifera* (Peck) Sacc. on mountain maple (*Acer spicatum* Lam. (1) and the subsequent description of *T. Dearnessii* Jenkins on red maple (*A. rubrum* L.) (4), the writers have had occasion to study for the purpose of identification a recent specimen of *Taphrina* on mountain maple.

#### HISTORICAL

Among the species of Taphrina occurring on North American maples, the earliest species to have been described is T. lethifera. for which the only record yet known is the type specimen collected by Peck (7) in the Adirondack Mountains of New York in 1886. This species possesses the largest asci of the five species of this group. Named in the order of size of ascus, from the largest to the smallest, the other four species are as follows: T. Aceris (Dearn. and Barth.) Mix (6) on Rocky Mountain hard maple (Acer grandidentatum Nutt.), the description of which was also recently emended (1); T. Carveri Jenkins (4) on silver or white maple (A. saccharinum L.); the previously mentioned T. Dearnessii Jenkins (4) on red maple, and T. Sacchari Jenkins (2) on sugar maple (A. Saccharum Marsh.) and on black maple (A. nigrum Michx.). Collectively, outline drawings of the asci of these five species showing their comparative size and form are contained in the articles just cited.

#### TAPHRINA ON MOUNTAIN MAPLE AND ON RED MAPLE NEAR ITHACA

The specimen of *Taphrina* on mountain maple under study was collected in the vicinity of Ithaca, New York, at Labrador Lake, on June 8, 1937, by the junior writer (Ray 345). On June 11, 1937, he collected a *Taphrina* on *Acer rubrum* both at Ringwood Preserve (Ray 350) and along Ellis Hollow Road (Ray 351), also in the vicinity of Ithaca.

As already indicated, *T. lethifera* on mountain maple and *T. Dearnessii* on red maple are evidently distinct, the ascus in the former species being much larger than in the latter. Peck states that *T. lethifera* may occupy part or all of the leaf, causing it to wrinkle, and that the asci covering the whole lower leaf surface may give it a glaucous appearance. He states that soon after infection the leaves turn black and sometimes all the leaves on a branch are affected, the fungus then causing a veritable blight.

While the *Taphrina* on mountain maple from the vicinity of Ithaca caused a certain amount of wrinkling and blighting of the affected leaves (FIG. 1, A and B), they were in appearance not unlike the specimens of *Taphrina* on red maple collected about the same time (FIG. 2). As will be shown presently, isolations were made from the fresh specimens of maple by the junior writer, and the resulting cultures were indistinguishable. This was before T. Dearnessii was described, and also before the characters of the ascus of T. lethifera were as well known as at present. It was at first assumed that the *Taphrina* on mountain maple was T. lethifera, and that on red maple the same species.

After the recent description of  $Taphrina\ Dearnessii$ , however, the writers made a critical study of the specimens from Ithaca, and compared them with the type specimen of T. lethifera and with authentic material of T. Dearnessii. In all cases the asci were entirely typical of the latter species so far as could be ascertained (FIG. 1, C and D, and FIG. 3). The asci of T. lethifera from the Adirondacks, were, as described, much larger than those of T. Dearnessii (FIG. 1, E and F). In making this comparison the writers found asci of T. lethifera on the upper as well as on the lower surface of the leaf, although they had not previously been so described.

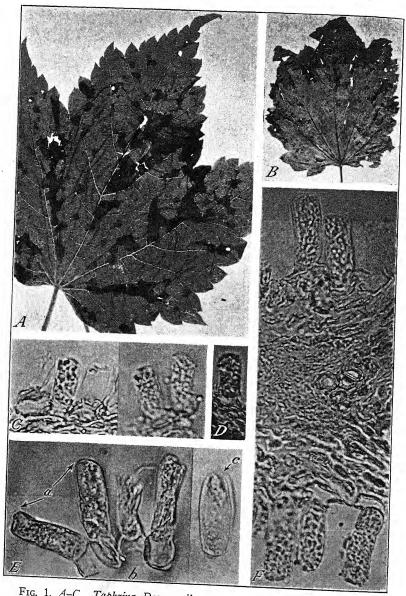


Fig. 1, A-C. Taphrina Dearnessii on upper (A) and lower (B) leaf surface of Acer spicatum from vicinity of Ithaca, New York, Ringwood Preserve, Coll. W. Winfield Ray (Ray 345), June 8, 1937. × 1. C, Asci of Taphrina Dearnessii from the specimen shown in A and B; D, from infected leaf of Acer rubrum, Lewis County, New York, June 21, 1927. Coll. D. S. Welch and G. H. Cumingham (4); E and F, Asci of T. lethifera

Isolations made at Ithaca, New York, from freshly collected specimens of Acer spicatum and A. rubrum were obtained by fastening lesions to the cover of petri plates. Spores discharged readily onto the medium in the bottom of the plate. Several days later colonies appeared scattered over the plate. From some of the isolated colonies transfers were made to tubes by means of a loop. The color of the colonies on potato-dextrose agar was a light pinkish-cinnamon, according to Ridgway's (9) color chart. The fungus grew well at temperatures ranging from 0° C. to 24° C., but growth was poor at 27° C. Fresh transfers when placed in 27° C. chambers retained their viability for 40–42 days. No growth occurred at 30° C., but healthy cultures placed in a chamber at this temperature remained alive for 10–12 days. No difference could be detected between the isolates from A. rubrum and A. spicatum in their culture characteristics.

Water suspensions of spores from actively growing cultures were atomized onto young leaves of several species of *Acer* during the spring of 1937. All attempts to produce infection artificially were unsuccessful.

From the foregoing study of Taphrina collected on mountain maple near Ithaca in 1937, it now seems that, for the present at least, this species should be considered as T. Dearnessii. With T. Sacchari attacking both sugar maple and black maple, there are now two species of Taphrina each affecting two different species of Acer. The present identification also shows that two species of Taphrina may affect the same species of Acer.

A similar type of behavior is shown by Taphrina on alder (Alnus) (8). Taphrina Robinsoniana Gies. occurs on the bracts of the female catkins of Alnus incana (L.) Moench. and A. rugosa (Ehrb.) Spreng. in the summer. Taphrina rugosa Ray also occurs on A. rugosa in the early spring. Taphrina amentorum (Sad.) Rost. occurs in Alaska on A. rubra Bong. (A. oregona Nutt.) and in Europe on A. glutinosa Gaertn. The female catkins of A. rubra in Oregon are also attacked by T. occidentalis Ray, while a new species, T. macrophylla Ray in litt., causes leaf-curl

on Acer spicatum, Elizabethtown, Essex County, New York, June 1886, C. H. Peck (Type); a, asci, b, basal cells. All  $\times$  500. Photographs in A and B, by W. R. Fisher, the others by M. L. F. Foubert.

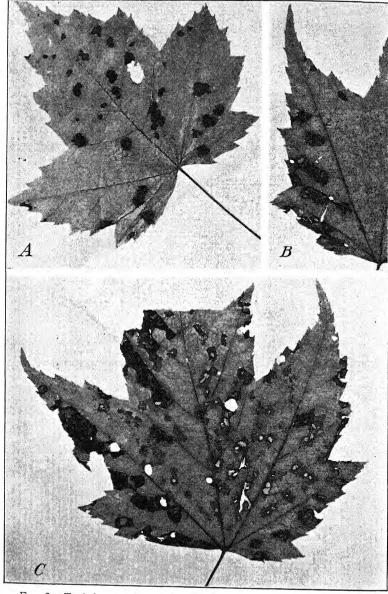


Fig. 2. Taphrina Dearnessii on Acer rubrum from vicinity of Ithaca, New York, (A) Ellis Hollow Road (Ray 351) and (B, C) Ringwood Preserve (Ray 350). Both collected on June 11, 1937.  $\times$  1. Photographs by M. L. F. Foubert.

of the same host in California. Thus A. rubra is an example of one host susceptible to three species of Taphrina. The female catkins of A. tenuifolia Nutt. and A. rhombifolia Nutt. may also

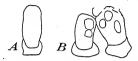


Fig. 3. Another comparison of asci of Taphrina Dearnessii from (A) Ascer spicatum and (B) Acer rubrum: X about 500.

be affected by T. occidentalis. Thus T. occidentalis is an example of a species capable of parasitism on three distinct forms of alder.

#### DISTRIBUTION OF TAPHRINA ON NORTH AMERICAN MAPLES

In addition to the present records of *Taphrina Dearnessii* from the vicinity of Ithaca, where the senior writer had collected it in 1927 (4), the junior writer has recently discovered the fungus on red maple in Oklahoma. Previously the fungus had not been

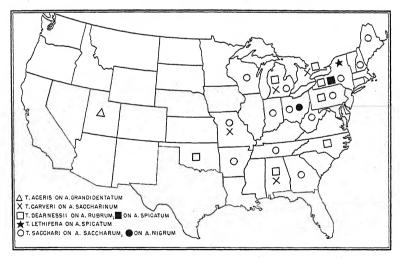


Fig. 4. Distribution of Taphrina in North America.

found west of the Mississippi River. Other westerly distribution records established during the past year for *Taphrina* species on maple are those of *T. Sacchari* in Wisconsin, based on a record of

1904 (3) and that of T. Carveri for Missouri based on a record of the current year (1939) (5). The known distribution of the group in North America is summarized on the map shown in figure 4.

#### SUMMARY

A species of *Taphrina* found on mountain maple in the vicinity of Ithaca, New York, in June 1937, is determined to be *T. Dearnessii* recently described on red maple from the United States and Canada. In the *Taphrina* group on North American maples, this is the second instance of one species infecting two different hosts, and the first of two species affecting the same host. The other species described on mountain maple is *T. lethifera* of which there is still only a single record from the Adirondack Mountains (1886). The first record of *T. Dearnessii* west of the Mississippi River, in Oklahoma, is given, and the present known distribution of the entire group is summarized on a map.

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STILLWATER, OKLAHOMA

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# NOTES AND BRIEF ARTICLES

SELENOPHOMA ON GRASSES 1

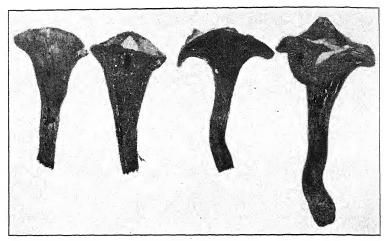
In connection with studies on Septoria spp. on Gramineae in the Pacific Northwest, it has been determined that certain fungi with nonseptate, falcate spores, borne in small globose pycnidia with coarse, globose peridial cells, were more logically assigned to Selenophoma Maire than to Septoria Fries. Accordingly, Septoria bromigena Sacc. on Bromus inermis becomes Selenophoma bromigena (Sacc.) comb. nov.; Septoria donacis Pass. on Arundo donax and other grasses becomes Selenophoma donacis (Pass.) comb. nov.—RODERICK SPRAGUE and A. G. JOHNSON.

#### CRATERELLUS UNICOLOR BERK & RAV. IN FLORIDA

The writer recently found this fungus in several different localities in central Florida and his notes may be of interest. The illustration, from a photograph kindly taken by Dr. G. F. Weber, is valuable because made from typical, fresh, well-developed sporophores. The species in question was originally described from specimens collected by Ravenel at Black Oak, S. C., in 1850 and distributed as No. 1406. According to Burt, the same fungus was found in Massachusetts by Dr. Francis and sent to Peck, who described it in 1899 as Craterellus corrugis. Coker in 1923 made both of these names synonyms of Clavaria pistillaris L.

On first seeing *C. unicolor* in the field, in Florida, the writer felt that he was looking at a new fungus; one quite different from the *C. pistillaris* he had so often collected in the northern states. When he examined the spores he found them to be, as Burt had said, much more slender than those of *C. pistillaris*. Young speci-

<sup>&</sup>lt;sup>1</sup> Cooperative Investigations between the Division of Cereal Crops and Diseases, Bureau of Plant Industry, U. S. Department of Agriculture, and the Oregon Agricultural Experiment Station. Published with the approval of the Director of the Oregon Experiment Station as Tech. Paper No. 332 Contribution from the Department of Botany.



Craterellus unicolor.

mens, to be sure, are difficult to distinguish but mature sporophores are usually much enlarged above, as shown in the accompanying illustrations. *C. unicolor* occurs in groups, usually in high-pineturkey-oak woods, growing in patches of leaves. The soil is sandy and sterile, moist during rainy periods but often quite dry. Always there is shade but it is never very dense.—W. A. MURRILL.

# A Key to Agarics

A graphic, illustrated, radially-arranged key to the principal genera of the Agaricaceae of the United States has been prepared for use by mycologists or others who have had less technical training. The key and a brief glossary of the terms used in the key were printed by the offset method on sheets of paper that measure  $25 \times 19$  inches. Single or several copies may be obtained without cost by writing to the Department of Botany, University of Missouri, Columbia, Missouri. Arrangements can be made for securing a greater number of copies.—John B. Routien.

# MYCOBIOTA OF NORTH AMERICA (Mycobiota of Mount Shasta)

During the past three summers it has been my pleasure to live at timberline on Mount Shasta in northern California. During this time I have collected a number of fungi, about 200 species, of which there was material enough in 75 collections for distribution in exsiccati form. Accordingly, during the past few months I have spent most of my time in preparing 25 sets of these fungi. The first 70 numbers of my first Century include these specimens and are now ready for distribution. Some of the specimens have been determined for me by various specialists. The specimens are accompanied by printed labels and are packeted in news-print since it is a low priced medium, and since many herbaria have their own standards in paper, size of packets, etc. A wide range of genera is represented. Several sets are still available. Further information may be had by writing the author.—WM. BRIDGE COOKE.

### MYCOLOGICAL SOCIETY OF AMERICA

SUMMER FORAY

The 1940 Foray will be held in the Mt. Katahdin region of Maine, August 20th to 24th, inclusive, with the collaboration of the Department of Botany and Entomology of the University of Maine. Headquarters will be at the High School in Millinocket. A member of the Foray committee will be at the High School on Tuesday and Wednesday to give such assistance as may be desired.

Millinocket is 105 miles north of Bangor by U. S. Route 2 to Mattawamkeag, and Maine 157 from there on. From Boston, Bangor can be reached entirely by the shore road, U. S. Route 1. A somewhat shorter route with somewhat better roads can be followed by leaving Route 1 at Brunswick, Maine, and going north to Augusta on U. S. 201, and then taking one of the two alternative routes from Augusta to Bangor. Those coming from others parts of New England or from states west can strike the excellent U. S. Route 2 through the White Mountains at any desired place across Vermont, New Hampshire or southern Maine.

Accommodations will be available as follows:

Great Northern Hotel, Millinocket—rooms with bath, \$2.50 a person; without bath, \$1.50 a person; meals a la carte.

Tourist homes in Millinocket—\$1.00 a person a night.

Kidney Pond or Bradeen Camps (new cabins), 30 miles northwest of Millinocket and 5 or 6 miles from Mt. Katahdin—\$5.00 a person a day double, \$30.00 a week (\$6.00 a day single). Mrs. Laura Bradeen, Prop., Millinocket.

Togue Pond Camps (individual log cabins), 18 miles from Millinocket, 12 miles from the top of Mt. Katahdin—\$4.50 a day,

\$28.00 a week. R. H. Crawford, Prop., Millinocket.

Yorks Camps at Daicey Pond, near the Kidney Pond Camps—no detailed information available, but probably of the same type, with rates similar to the preceding ones.

Chimney Pond in Baxter State Park, for those who wish to rough it, with water, fuel, cooking utensils and lean-to's available (but food and blankets not provided), about 25 miles from Millinocket and a little over 3 miles by trail from the end of the auto road.

Several other camps on lakes not directly accessible by auto. Two restaurants in Millinocket.

The laboratories of the Millinocket High School have very graciously been placed at the disposal of the Society for the care and study of the fungi collected.

Further information concerning accommodations, fishing, mountain climbing, etc., can be obtained from the Chamber of Commerce in Millinocket; from Dr. F. H. Steinmetz, Department of Botany and Entomology, University of Maine, Orono, Maine; or from the chairman of the Committee at Brown University, Providence, R. I.

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# **MYCOLOGIA**

OFFICIAL ORGAN OF THE MYCOLOGICAL SOCIETY OF AMERICA

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No. 4

# EVOLUTION OF THE BASIDIOMYCETES AND ITS RELATION TO THE TERMINOLOGY OF THE BASIDIUM

DAVID H. LINDER 1

(WITH 6 FIGURES)

Within the past fifteen years especially, but dating back to Patouillard's (1900) work on the classification of the Basidiomycetes, interest in the morphology of the basidium has increased greatly. This is to be expected when that fundamental structure, because of the increased importance placed upon microscopical characters, has come in for careful scrutiny. Since the basidium is an integral and a most important structure in relation to the nuclear cycle of the forms, it is obvious that its fundamental nature should make it a logical organ in which to search for characteristics to employ for the separation of this large class of fungi into the smallest possible groups, and at the same time to show their natural relationships.

It seems unfortunate, however, once the characteristics of the basidium have been fairly completely learned, that there must also be an increase in terminology beyond our actual needs and as a result mycologists are faced with the necessity of endeavoring to ascertain exactly what various writers mean when they apply the terms probasidium, hypobasidium, promycelium, metabasidium, epibasidium, and sterigmata in the various orders of the Basidio-

<sup>1</sup> Contribution from the Laboratories of Cryptogamic Botany and the Farlow Herbarium, Harvard University, no. 182.

[Mycologia for May-June (32: 275-418) was issued June 1, 1940]

mycetes and more especially in the lower groups. To the writer it seems that the greatest service is rendered, not by the creation of new names, but by the employment of the smallest number of terms that are compatible with a clear and consistent definition. For this reason, then, the older terminology seems amply to satisfy the needs of the investigator. Thus the term probasidium is fully adequate to describe the resistant bodies represented by the teleutospores of the Uredinales (or in exceptional cases the aeciospores), the chlamydospores of the Ustilaginales, or the more or less resistant bodies of the Auriculariales. The name basidium then would be applied to that structure which is in part the homologue of the ascus and which, following caryogamy and meiosis, bears the spores either directly or indirectly through the interpolation of the sterigmata. Recognizing that there are variations, it may be necessary to have further refinement of terms and to utilize such terms as phragmobasidium in connection with the type of basidium presented by the Uredinales, Ustilaginales, and Auriculariales, or cruciate basidium for the Tremellales, and holobasidium for the higher Basidiomycetes. If there is interpolated between the probasidium and the basidium a mycelial phase which may be more or less extensive, as is true in the genera Helicogloea or Myxomycidium, or even in some species in the Uredinales, it is sufficient to realize that the basidium is stalked and to speak of that structure as the basidial stipe. This stipe is not a new structure of fixed length for a given species, but rather varies in length according to conditions of the environment. Thus in Gymnosporangium Nidus-avis, if the spores are germinated in water, it will be found that the stipe of the basidium arising from those teleutospores that are near the surface of the water are very short, whereas the stipe arising from teleutospores more deeply immersed are proportionately more elongate. Similarly, when probasidia are deeply immersed in a gelatinous matrix, as in Helicogloea, the length of the stipe is proportional to the depth to which the probasidium is immersed. The writer is in agreement with Martin (1938) when he writes, "It seems clear that Boedijn's contention that the two parts of the basidium in H. indicum are separate organs can not be admitted." Finally, the term sterigma, which like the basidium has been refined almost beyond recognition, would

be applied to that structure which arises from the basidium and bears the basidiospore. Because of the homologies to be pointed out later in this paper, the restriction of the sterigmata to apply only to that portion of the spore-bearing filament which is very slender and through which the nucleus squeezes in its passage to the spore, not only leads to confusion but is illogical. The same arguments used against considering the basidial stipe as a distinct organ are applicable here,—namely its development and its length are dependent on environmental factors such as immersion in a surface film of water or immersion of the basidium in a gelatinous matrix. Thus in this respect the writer is in full support of Boedijn's statement (p. 194, 1937) that "Now it is clear that the 4-celled part [of the basidium of the Tremellales] certainly is homologous with the 4-celled basidium of the Auriculariaceae; only the septation is different, being vertical instead of transverse. According to the theory of Neuhoff we are forced, however, to accept the hypobasidium as one-celled and the epibasidium as 4-celled for the Auriculariaceae and just the reverse for the Tremellaceae." A glance at a section of the hymenium of Auricularia Auricula-Judae or a germinating teleutospore would show immediately the futility of Neuhoff's (1924) concept of what a sterigmata should be. This, even without the homologies to be pointed out later, is sufficiently inconsistent to drive one back to the old-fashioned concept of the sterigmata.

To make clearer the application of these terms, and to lend supporting evidence, it seems necessary to survey the origin of and the evolutionary trend within the Basidiomycetes. Before commencing this survey, however, it should be strongly emphasized that today we are dealing not with organisms that are the result of recent modification, but those which are in reality the end products of a long line of evolution in which the ancestral forms have been lost. As a result, today we can deal only with those forms which have retained some, or possibly all, of their primitive characteristics. For this reason the writer wishes to emphasize that when it is stated that one genus or group arose from another, the implication is in reality that what is considered to be the primitive form as it is found today, behaves in much the same manner as its hypothetical and geologically more ancient

progenitor, and not necessarily that a stated present day species or genus has given rise to another. Because of the almost complete lack of fossil evidence, it is necessary to evaluate the evidence that is furnished by living forms, a fact that has not been sufficiently kept in mind and which has led to many and often conflicting ideas in regard to the phylogeny of the Basidiomycetes. In order to obtain not only a standard nomenclature for the basidium and related parts, but also to secure a stability in taxonomy, it is necessary to accumulate as much evidence as possible so that from it there may be sorted out the material which will serve to build the basic structure of the much-to-be-desired system of natural classification. It is the writer's hope that the ideas expressed in the following pages may contribute to some extent towards this end.

# ORIGIN OF THE UREDINALES

Where should we look for the ancestral forms of the Basidiomycetes? Because of the striking analogy shown by diagrams of the life-history of certain members of the red algae and of the Uredinales, it has more than once been suggested that we look for ancestral types in the Rhodophyceae. Without going into too great detail, this source may be discarded for several reasons which may be listed briefly as follows: (1) those forms of red algae which show the greatest similarity of life-cycle to that of the Uredinales are all marine, (2) the chromosome number of the red algae is greater than that of the Basidiomycetes, (3) nuclear division takes place in quite a different fashion, and (4) the life-cycles, while paralleling to a degree those of the Basidiomycetes, are analogous, not homologous, since the alternation of generation in the red algae, for the most part, involves two separate types of plants, one having N-chromosomes, and the other 2-N, whereas in the Basidiomycetes the cycles involve an N-chromosome phase and an  $\mathrm{N}+\mathrm{N}$ phase in addition to the 2-N phase which, relative to the red algae, is only momentary.

The other alternative to the red algae as the ancestral stock of the Basidiomycetes is the Ascomycetes. This hypothesis, as may be ascertained from a perusal of the more recent literature, is becoming more generally accepted, and not without good reason, since the Basidiomycetes represent a culmination of an evolutionary trend that began very early in the evolution of the Ascomycetes, namely the increasing importance of the dikaryotic phase that is interposed between plasmogamy and caryogamy. This trend and the homologies between the crozier cells and the clamp connections, and between the ascus and the basidium as has already been pointed out by Gäumann (1926) and further emphasized by Rogers (1934) and others, seem sufficient to warrant the assumption of an ascomycetous ancestor for the Basidiomycetes.

Among the ascomycetous forms, Ascocorticium has been considered to represent a possible point of departure. The reasons for the choice of this genus as a starting point are admirably summed up by Rogers (1934) as follows: "Although there is no incontrovertible evidence that the evolution of the basidium has at any level been monophyletic, yet the numerous fundamental similarities among the various basidial types speak for their origin from an at most greatly restricted ancestral group. The complete series of basidial types being represented in resupinate forms only, it is proper to reason that the greater part of the fundamental morphological evolution has occurred at this level of development, and also to postulate the rise of the Basidiomycetes from such resupinate form as Ascocorticium. Further, the sterigma-spore relation, as has been shown by Buller, is morphologically and physiologically a fixed one throughout the gymnocarpous basidiomycetes; this being the case, it has either developed de novo-and scarcely more than once—in the course of basidial evolution, or else it represents, likely in a modified form, a biological adaptation already present in the ancestral ascomycete. The first implies development of all basidiomycetes from a single basidiomycetous ancestor; polyphyletic evolution of the group has any considerable probability only under the second hypothesis." The writer is in hearty agreement with the suggestion that the Basidiomycetes are probably monophyletic in their origin, but cannot agree that the resupinate character, even though associated with all the different basidial types, must needs point to an Ascocorticium-like ancestor since it seems more than likely that the resupinate character may not only develop independently among the different groups, but also that it is a secondary development and derived from the pulvinate type of fructification.

It is the writer's belief that the Uredinales or an ancestral form of this order should be considered to be the primitive Basidiomycetes. On this basis, the ascomycetous ancestor would possess the following characteristics: during the life cycle it should produce pycnidia with receptive or "Woronin hyphae," it should have one or two additional conidial forms, and possibly it should be parasitic. These qualifications are met by the Pyrenomycetes and among these the order Dothideales, in its older and more general sense, may well be suggested as a starting point, although for the purposes of the present discussion the exact allocation of the ancestral form serves no useful purpose since the issue is not where but how the Basidiomycetes arose from the Ascomycetes.

The demonstration of the nature of the pycnidium by Craigie (1927) suggests, and the subsequent work by Allen (1934), Andrus (1931), Hunter (1936) and others emphasize the remarkable parallelism between the rusts and the Ascomycetes. parallelism is so remarkable that it cannot lightly be dismissed, as is done by those who would derive the rusts from the Corticium or Tulasnella-type of basidium. Wolf (1935) has shown that the pycnidium of the dothideaceous Cymadothea possesses receptive hyphae that are exactly homologous with those figured for the rusts. Indeed were the connections with the perfect stages not previously known, it would be difficult if not impossible to tell the ascomycetous and the uredinaceous pycnidia apart. A comparison of the mechanism of fertilization may be carried even further as a result of the recent excellent investigations of Backus (1939) who has shown that the "Woronin hyphae" or receptive structure of Neurospora may be extremely elongate and branched, and this structure may well be compared with the stomatal hyphae which are reported in the Uredinales. The exact reproduction in the rusts of the methods of fertilization, and of the structures associated with this process, in the Pyrenomycetes should serve as the strongest evidence for relationship between the two groups. If, then, it may be assumed that the pycnidia of both classes of fungi are homologous, it is only necessary to postulate that during the course of time and as a result of various environmental factors, many forms survived in which the sequence of spore types became fixed. Thus the pycnidia were produced first, and as a result

the conidial types, as exemplified by the aecidiospores and uredospores, have come to be dikaryotic bodies for the dissemination of the organism during periods favorable for growth. This hypothesis is not made without some justification, for, as already pointed out, the trend within the Ascomycetes has been towards the increase in the duration and importance of the dikaryotic stage of the life-cycle, a trend that is continued in the rusts when the spores, aecial and uredo of the present day forms, became dikaryotic. The spores thus equipped with nuclei of the opposite sex factors serve to spread the fungus more rapidly since, both factors being present, the thallus may immediately proceed to the formation of the zeugites or resistant structures with the onslaught of unfavorable conditions, thereby not only facilitating spread, but also the survival of the fungus. Thus it may fairly be stated that increased emphasis is placed on the dikaryon phase.

The comparison between the Ascomycetes and the Basidiomycetes may be pursued further and the asci may be compared with the teleutospore of the rusts. In many genera of the Inoperculate Ascomycetes, as in Parodiopsis, Myriangium, Leptosphaeria, Mycosphaerella, and in other more distantly related genera, there are many species of which the asci are characterized by an apical thickening of the wall and in that thickened portion there is provided a large pore-like modification of the wall which is comparable to that found in the teleutospores of Melampsora, Uromyces and many other genera of the Uredinales. If the asci of this type, that is, with the thickened wall and provided with an apical pore-like modification, were formed without the protection of the perithecium, mutual pressure as well as pressure exerted against the epidermis of the host would result in the formation of a palisade-like layer that would be comparable to that found in the rusts of today as exemplified by species of Melampsora. Presumably the hypothetical ancestral form may originally have germinated as do many of the living species of Pyrenomycetes. The asci of species of Pleospora, Leptosphaeria, Sporormia, and Melanomma, according to Ingold (1933), are provided with a rigid outer wall and a thin elastic inner wall. Upon germination, the pore-like modification at the apex of the asci is either greatly softened or ruptured and the inner wall then emerges through the resulting pore with almost explosive rapidity (FIG. 1); thus the spores are protruded beyond the rigid ascus wall still within a slender membrane, a condition that foreshadows the development of the basidium of the rusts. In the Uredinales there is a delay

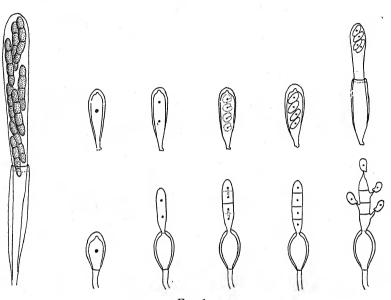


Fig. 1.

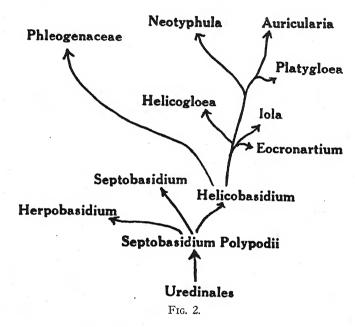
in nuclear division until the germ-tube, which is the counterpart of the thin-walled internal ascus, has grown through the pore and the nucleus and accompanying protoplasm have migrated into this structure. Nuclear division then takes place, but each nucleus, instead of becoming surrounded by a wall as in the Ascomycetes, becomes separated from the others merely by a cross-wall. Thus the same four-celled structure is found in the rust basidium as is found within the extruded inner elastic wall of the Ascomycetes, but instead of being represented by free spores, they are represented by cells.

The above derivation of the basidium seems to explain the fixity of the number of cells of the majority of the lower Basidiomycetes, namely four, and is all the more comprehensible if the derivation is from an ascomycetous ancestor in which four-sporedness had become a relatively fixed characteristic. The substitution

of cross-wall formation in the basidium for free-cell formation as in the ascus does not seem to be an insuperable barrier to accepting this method of origin. If, on the other hand, the basidium were derived from an Ascocorticium-like ancestor with a thin-walled ascus, it would be necessary to postulate, as Neuhoff (1924) does, that the homobasidial types were derived first and then during long periods necessary for the evolution of the rust types, the basidia went through stages of transformation exemplified by the genera Gloeocystidium, Kordyanella, Iola, Cystobasidium, and Uromyces to Puccinia which according to this system would place the Uredinales in highest place. In so deriving the group, the highest form is that in which the method of fertilization is characteristic of the Ascomycetes. If such were the line of evolution, it may be remarked that Mother Nature wasted much time and a golden opportunity to attain her ends with much less difficulty. Another objection to using the holobasidium as a starting point for the remainder of the Basidiomycetes is that it is necessary to imagine that the formation of sterigmata came about as a result of the terminal proliferation of the ascus in the manner illustrated by Taphrina in which Sadebeck (1884) found that young asci under certain conditions germinate with sprout mycelia upon which conidia were formed. However, it should be pointed out that the asci were still young and had not as yet differentiated ascospores. Under such conditions, it would therefore seem that in immature asci when subjected to a definite set of conditions that favor vegetative growth, the reproductive processes are suppressed and the vegetative phase becomes reestablished. If this is correct, then it would be difficult to derive the basidium, which is strictly a result of reproductive activity, from the ascus in this manner. In view of the fixity of the position, number, and nature of the sterigmata on the basidium, it hardly seems probable, especially in view of the fact that in Taphrina at least, the process of spore formation is that of budding, and not of extrusion and eventual discharge as is true for the basidiospores. In the sense of the budding by the ascus, the basidium is not a proliferative structure since, with but a few exceptions, once the basidium is formed, it contains the entire content that was formerly in the probasidium, as eventually do the spores. If the basidium were proliferative in nature, then BENEZIA :

it should retain at least a portion of the protoplasm so that additional spores might be formed in succession. In this respect, the basidium closely agrees with the ascus.

It may be objected that the absence of clamp connection in the Uredinales prevents this order from being an ancestral group from which the other members of the Basidiomycetes may have been derived. It has not been definitely proved that clamp connections may not be present in the rusts. Even though this were conclusively proved, we have no way of demonstrating that such structures were not present in the early forms. It may be that the ancestral forms did have clamp connections, but because of the fact that the group has been intramatrical over an extremely long period the clamp connections as a consequence have been lost. A parallel to this situation exists today, for Greis (1938) and others have shown that in the Polyporaceae, the mycelium that is imbedded in the substratum, even though dikaryotic, does not produce clamp connections, yet once outside in the air they may be formed on the mycelium in relative abundance, thus suggesting an oxygen relation. However, a physiological explanation is not necessarily as important as it may appear to be, for an explanation may readily be found in the phylogeny of the group. If, as has been proposed above, the Uredinales are derived from a pyrenomycetous ancestor, there is no need for supposing that clamp connections have as yet developed. Crozier formation in certain members of what formerly was the order Dothideales, is not at all well developed nor is it highly developed in many of the Sphaeriales. It is not until the higher families of the Inoperculate Discomycetes that crozier formation has become well fixed, and in the higher of these groups even clamp connections may be found in the vicinity of the hymenium. Thus it may be said that crozier formation becomes important when a large number of asci result from a single or relatively few acts of fertilization. The structure therefore facilitates proliferation and the formation of numerous reproductive bodies (asci). It should be remembered that the mycelium subtending the fruiting bodies of the Inoperculate Discomycetes is haploid. In the rusts, the need for proliferation within a limited fructification is absent since dikaryotization takes place early in the life-history and as a result the proliferative service of clamp connections has not yet become necessary. Since the species are parasitic, and since the substratum is relatively abundant, the need for the production of a vast number of basidiospores is not so great. Even though the host were not abundant, the dikaryotic conidia serve equally well to insure the spread of the parasite. With the shortening of the life cycle and with the change from parasitic to



a saprophytic or symbiotic mode of life, the need for proliferation comes in since then the fruiting body becomes more extensive. Thus we find that for the first time, Septobasidium and Helicobasidium, for example, produce large numbers of probasidia over an extensive area, and in these genera, except in those species in which the tendency towards homothallism enters to confuse the picture, clamp connections are present for the first time. The absence of clamp connections, if this be true, in the Uredinales, may then be explained by stating that in regard to these structures, the rusts have reached a degree of development parallel to that found in the higher Pyrenomycetes but slightly lower than that in the Inoperculate Discomycetes.

Further consideration of the phylogenetic trends within the

Uredinales, excepting as it is relative to the origin of other groups, is superfluous here in the light of the many papers on the subject by Arthur (1929), Cummins (1936), Cunningham (1931), Dietel (1938), Faull (1929), Hiratsuka (1936), Jackson (1931), Mordvilko (1926) and others. The morphology of the basidium within the order is comparatively constant and this in spite of the fact that nuclear behavior, as a result of the trend towards homothallism, may be extremely variable. It is this variation in nuclear behavior, in addition to the shortening of the life-cycle, that makes possible the derivation of the remaining Basidiomycetes from the rusts. For convenience and brevity, only three evolutionary lines will be discussed and these in the order listed: (1) Uredinales—Auriculariales—Dacryomycetales, (2) Uredinales—Ustilaginales, and (3) Uredinales—Tremellales—Autobasidiomycetes.

## UREDINALES—AURICULARIALES

In a previous paper, the writer (1929) in discussing Saccoblastia intermedia [Helicogloea intermedia (Linder) Baker] indicated that the Auriculariales appeared to be derived from and are not ancestral to the rusts. Since that time additional evidence has accumulated to confirm this view. Craigie's (1927) exposition of the nature of the pycnidium was followed by a series of papers demonstrating the method of fertilization in the rusts, and Ames (1932, 1934) and Drayton (1934), to name but two investigators, by showing that spermatization takes place among the Inoperculate Ascomycetes (here employed to include both the Pyrenomycetes and Inoperculate Discomycetes) have demonstrated the identity of the methods of fertilization in the two groups of fungi. During this period also, Jackson (1931) has clearly indicated that the evolutionary trends within the Uredinales all lead towards the shortening of the life-cycle, and in a later paper (1935) has shown that to a marked degree there is a correlation between this trend and a change from heterothallism to homothallism. There may be a question as to whether it was the change of hosts during the course of evolution or the shortening of the cycle that has led to homothallism. Whichever is the cause, it is sufficient at this point to realize that changes in nuclear behavior, in morphology, and in life-cycles has taken place and has been expressed in different manners by different members of the group. If then the long-cycle forms are considered to be primitive, it would indeed be difficult to derive the rusts from the Auriculariales. None of the members of that order, so far as the writer is aware, possess pycnidia in their life-cycle and therefore to derive the Uredinales through the highest forms, that is to say, those forms with an abbreviated life-cycle and in which their nuclear behavior has become quite variable as a result of the trend towards homothallism, and to expect evolution to proceed backwards towards those forms with a long cycle which are considered by most Uredinologists to be the most primitive, is illogical to say the least. For this reason and for others already outlined, it becomes necessary to consider the Uredinales as the ancestral group from which sprang the Auriculariales.

As has been stated repeatedly, the Uredinales have proceeded from the complex to the simple life-cycle. During the evolutionary change, not only have spore forms dropped out in various fashions, but correlated with this to a remarkable degree, it would appear that spermatization also has tended to fall by the wayside and the pycnidia and pycnidiospores to become functionless or obsolete, thus leading to dikaryotization through hyphal fusions in the manner described by Christman (1907) for *Phragmidium Potentillae-canadensis*, and by other investigators for other rusts in different genera. When spermatization takes place in the higher short-cycle forms, then it is more than likely that the rôle of pycnidiospores has been taken over by the secondary sporidia produced by the basidiospore or by hyphal fusions. Whatever the mode of fertilization in the short-cycle rusts may be, the trend within the order seems to be towards the Auriculariales.

Another tendency towards the Auriculariales is shown to some degree by the genera *Cystospora* and *Tranzschelia* of the Pucciniaceae, and to a conspicuous degree by *Goplana mirabilis* of the Coleosporeae—namely the extramatrical production of the probasidium and the tendency towards exoparasitism. It is not beyond the realm of probability to consider that these forms of today merely duplicate what has taken place in the geologic past, and accordingly the Auriculariales as represented by *Septobasidium Polypodii* Couch (1929) and by *Uredinella coccidiophaga* Couch

(1937) may be considered to be derived from ancestors which at an early date became extramatrical. With the exception of S. Polypodii and another undescribed species that has been observed by the writer, the genus Septobasidium early changed from an external parasite on the host plant to a parasitic symbiont of scale insects, a change that has become a relatively fixed characteristic of the genus. However, from the S. Polypodii type of ancestor there has also arisen a line that leads directly to Helicobasidium and Cystobasidium and it is characterized by the increasingly saprophytic mode of living. Within the genus Helicobasidium, just as in Septobasidium, there is a tendency towards homothallism or parthenogamy, if we compare it with the parallel situation illustrated by the Endomycetales and Saccharomycetales, and at the same time there is a gradual loss of the probasidium. These two characteristics do not necessarily go hand in hand since there is also an evident loss in the development of the probasidium in the heterothallic species which, it would seem, gave rise to the higher Auriculariaceae, as is indicated in the accompanying phylogenetic scheme. The Phleogenaceae would appear to have been derived from an ancestral species in Helicobasidium that had already lost the probasidium and at the same time has become more or less saprophytic. On the other hand, Iola, as shown by the accompanying chart, still exhibits the probasidium and may be considered to be parasitic. The genus on the one side seems to be ancestral to Eocronartium which is parasitic on mosses, and on the other to Helicogloea which to a degree still produces probasidia but at the same time is saprophytic or in some instances may be parasitic. This latter genus appears to be a side branch, but possibly it may have given rise to Platygloea and eventually to Neotyphula and Auricularia which are mostly saprophytic forms that have developed more complex fruiting bodies and at the same time have lost the definite probasidial structures that are present in the lower groups.

Returning again to the *Septobasidium Polypodii* ancestral type, it would appear that from this has arisen the monotypic genus *Herpobasidium*, a genus which, although parasitic, nevertheless has lost the probasidium and has proceeded towards the homothallic condition described by Jackson (1935). With this tendency to-

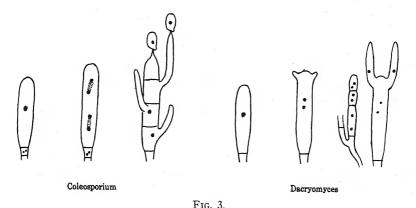
wards homothallism, there have been introduced irregularities in nuclear behavior and at the same time changes in the structure of the basidium with the result that that structure resembles the basidium of Dacryomyces. It seems doubtful, however, that Herpobasidium has given rise to any further groups, although such a possibility cannot be definitely excluded. The reasons for considering Herpobasidium to be the end of an evolutionary line will be discussed in a following paragraph. For the present it will suffice to sum up the origin and evolution within the Auriculariales by pointing out in the accompanying diagram that those forms with the characteristically coiled haustoria, such as are present in some of the Uredinales and are well illustrated in the genus Septobasidium, are closely allied, that they are arranged according to the decreasing importance of the probasidium, and finally that the parasitic forms are grouped together and are considered to be more primitive than the saprophytic forms.

Before entering a discussion of the origin of the Dacryomycetales, mention should be made of the part played by parasitism or saprophytism in evolution, since much has been written upon this subject, and for the most part there has been a tendency to look upon the parasitic mode of living as something fixed and unchanging. For the present day members of the Peronosporales and the Uredinales, this seems to hold. However, it should be kept in mind that these present day obligate forms are the result of long ages of selection and evolution towards specialization. There are other groups which also show specialization of parasitism as is exemplified by the genera Sclerotinia and Mycosphaerella, to name but two, and yet these forms may readily be grown in culture. The same is true of the Ustilaginales. Even in the rusts there is evidence that there may be a tendency away from strict parasitism, since the writer has observed in the field that some species continue to produce fruiting bodies after the host substratum has passed a stage that would most liberally be termed senescence. Thus teleutospores of Uromyces Fabae have been observed to be formed in the autumn on stems of Vicia cracca which had apparently been killed in late summer by the uredo stage. If this can happen today after the forms have gone through long ages of host specialization, then why could not forms become weakly parasitic or saprophytic during a much earlier period when the characteristics had become less well fixed and when the species were in a young and more "fluid" state? Newton (1939) has stated that "Certain pathogenic characters (infection types) have proved dominant over others, and the distribution of the characters in  $F_2$  and subsequent generations has suggested Mendelian inheritance." If parasitism is a result of Mendelian factors and also, as was suggested in the same paper, may be influenced by the cytoplasm, then the chances are fair that during the ages, mutations could have occurred which gave rise to weakly parasitic or even saprophytic species.

### DACRYOMYCETALES

The relationship of the Dacryomycetales to the Auriculariales is indeed dubious and it is considered here only because in the genus Herpobasidium there is found one clue as to the manner of origin of the non-septate basidium. Reference to Lind's paper (1908) or to that of Jackson (1935) will demonstrate that in Herpobasidium the basidium is two-celled and that the two sterigmata often parallel each other. Thus if the basidium were to lose its single septum, the forked basidium would result. According to Dangeard's (1895) interpretation of the cytology of the basidium, such a derivation would be acceptable since then it would be necessary to postulate only the loss of the basidial septum and the survival of but a single nuclear division. However, Juel (1898) studying the same species, Dacryomyces deliquescens, found that the fusion nucleus, instead of dividing but a single time, divided twice to produce four daughter nuclei of which two migrated into the spores. These results of Juel have further been substantiated by the work of Gilbert (1921) who studied an undetermined species of Dacryomyces, and by Bodman (1938) who investigated the cytology of Guepinia Spathularia. By correlating observations made on the Uredinales in which the four-nucleate basidium is considered to be the more primitive, it would be impossible to derive the four-nucleate dacryomycetaceous basidium from the binucleate Herpobasidium type which has already passed through stages of reduction to reach this condition. It therefore is necessary to look elsewhere for the ancestral type. Since the basidium is four nucleate in those dacryomycetaceous forms that have been

studied, since binucleate conidia comparable to aeciospores are often present, and also since the characteristic yellow-orange pigment that is common to both groups is present, the relationship to the Uredinales seems closer than the morphology of the basidium would at first glance lead one to suspect. If on these grounds the



relationship with the rusts is as close as it would appear to be, the affinity would probably be not with the Pucciniaceae because of the well developed probasidium in that family, but more likely would be with the Coleosporeae in which the probasidium is directly converted into a basidium (FIG. 3). To derive the Dacryomycetales from this source, it would be necessary to conjecture that the progenitors were forms that had become saprophytic in their mode of life, and that the sorus had become imbedded in a more copious gelatinous matrix. At the same time, as a result of variations in nuclear behavior similar to those already mentioned, the septa have been lost, although the double division of the fusion nucleus still persists,2 even though but two of the four daughter nuclei migrate into the sterigmata and eventually into the basidiospores, while the other two remain behind in the basidium and degenerate. According to this theory, the sterigmata are not special organs to be labelled epibasidia but in fact are exactly homologous with those of the Uredinales or the Auriculariales, and

<sup>&</sup>lt;sup>2</sup> It is possible that Dangeard investigated a species other than *D. deliquescens* or else a homothallic strain of that species, the fusion nucleus of which failed to divide twice.

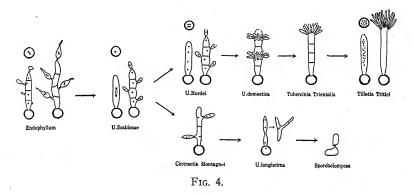
like those of the latter group they vary in length in proportion to the depth to which they are buried in the gelatinous matrix. That their number is constantly two to a basidium is explained by the fact that the basidium has lost its septa and that nuclear behavior has become so modified that only two of the four daughter nuclei are functional.

It is questionable whether the order Dacryomycetales has given rise to other groups of the higher Basidiomycetes since the nuclear behavior and the structure of the basidium appear to set the order apart as a distinct group that ends an evolutionary line. Accordingly, although the basidium is homobasidial in structure, it is phragmobasidial in nature. Thus the order finds a logical place among the Protobasidiomycetes. Within the order, further evolution has proceeded in two directions, the first from the pustulate forms of Dacryomyces to the resupinate genus Ceracea and then to Arrhytidia which may be more or less resupinate but with free margins, or more or less saucer-shaped. The other line of evolutions is towards the stipitate fruiting bodies and begins with Dacryomyces, goes through Guepinia and Dacryomitra on the one hand, and Calocera on the other. Thus the order of development closely parallels that of the Auriculariales and, in fact, the other groups of the Basidiomycetes in which there is any considerable degree of variation in the shape and size of the basidiocarp.

### USTILAGINALES

For the origin of the Ustilaginales it is also necessary to turn back to the Uredinales. It again is evident that the group has resulted from the shortening of the life-cycle of the rusts, but in this instance it is necessary to look for the place of origin not in the short cycle forms which produce typical teleutospores, but rather in the endo-forms in which the aeciospores have taken over the function of the probasidium. Since there is no reason why teleutospores should not be dropped out of the rust life-cycle just as have the aeciospores and uredospores, the chlamydospores of the smuts are considered to be identical in nature with the aeciospores of the endo-forms, and like them to germinate by means of a characteristic basidium. Evidence for the derivation of the smuts from the rusts in this manner is furnished by species similar to

Endophyllum Euphorbiae-sylvaticae, in which Moreau (1919) has shown that the paired nuclei, without fusing in the probasidium, pass into the young basidium, divide and become separated by septa to form a four-celled basidium. The daughter nuclei migrate into the basidiospores and then divide or else they may divide prior to their migration, but in either case the entire content of each basidial cell passes into the spores. It will be recalled that



in certain of the Ustilaginales the nuclei fuse prior to the formation of the basidium, and also that during the process of spore formation, the nucleus in each basidial cell divides, one daughter nucleus passing into the spore while the other remains behind to divide further and produce other spores. In these two main aspects, the forms represented by species of Endophyllum and present day Ustilaginales are distinct, yet it is not difficult to imagine an Endophyllum-like ancestor in which caryogamy takes place prior to basidial formation and then when the basidium has formed, the nuclei divide in the basidial cells, one of which resulting nuclei passes into the spore while the other remains behind to carry on in a manner identical with the present day smuts. Such a form would be exactly intermediate between the rusts and the smuts, and in view of the great diversity of nuclear behavior in the two groups, it is not difficult to imagine such a form as existing today or as having existed in the past. Aside from the resemblance between the aecial type of teleutospore and the so-called chlamydospore, there is also a similarity in methods of fertilization. According to Hanna (1929), although infection of the host by single germinating spores takes place, there is no formation of chlamydospores (or probasidia) until there is fusion between spores or between mycelium of opposite sex potential, a fact that would be expected according to the hypothesis that when spermatization disappears, plasmogamy takes its place. The fusion of secondary basidiospores or sporidia seems to be a later development that has arisen since the Ustilaginales were derived from the Uredinales, and the trend towards fusion of the spores on the basidium not only represents an advancement of the position in the life-cycle of dikaryotization but also represents a more efficient method for assuring the dissemination of the species, since it has resulted in the insurance that nuclei of opposite sex potential meet in a less accidental fashion than would be true if the spores germinated individually and relied on chance for mycelia of opposite sex potentiality to meet.

On the assumption that the Ustilaginaceae were derived from an endo-form of the Pucciniaceae as a result of the aeciospores taking over the functions of the teleutospore and also as a result of a slight change in nuclear behavior, the Ustilaginaceae would appear to be more primitive than the Tilletiaceae. Within the former family, evolution appears to have proceeded in two lines: towards the formation of a coenocytic basidium and the apical production of basidiospores, and in the other direction towards the reduction of the basidium.

Following the first line of evolution within the Ustilaginaceae, there is an evident trend from the typical ustilaginaceous basidium in which, like those of the rusts, the first and second division of the fusion nucleus takes place within the basidium, and the spores are produced one at a time on each basidial cell. This is exemplified by Ustilago Scabiosae which was studied by Harper (1898). The next step is shown by Ustilago Hordei in which both the first and second divisions of the fusion nuclei take place, not in the basidium, but in the probasidium, thus advancing the place and time of meiosis, although basidiospores continue to be produced singly on each basidial cell. Slightly more advanced is Ustilago domestica since, instead of producing the basidiospores singly and successively on each cell, the spores are formed in greater numbers and almost simultaneously on the basidial cells as is shown in fig-

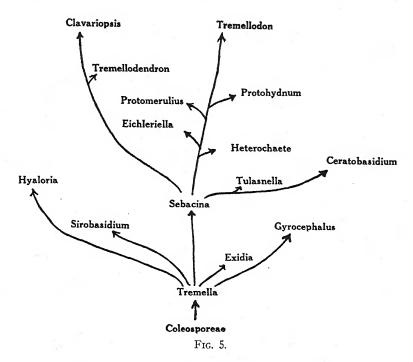
ure 4. In addition to this, the spores are definitely localized so that a ring of spores is produced at the basal end of the outermost cell, the apical end of the second cell, the basal end of the third cell and the apical end of the fourth cell in such a manner that fusions, since sex segregation has taken place in such a manner that nuclei of opposite sex factors are in adjacent cells, may take place readily between opposing spores. The next step in advancement, shown by Tubercinia Trientalis of the Tilletiaceae, leads to the localization of the basidiospores to the apex of the basidium which is still septate. The final stage in the evolutionary line is reached in Tilletia Tritici where most of the divisions of the fusion nucleus take place in the probasidium with a few occasionally occurring in the basidium which is usually non-septate and proceeds directly and efficiently to acrogenous basidiospore formation. Fusion between the spores occurs while they still remain attached to the basidium. As is summarized in figure 4, the trend has been from the septate to the non-septate basidium, from a single division following meiosis to several, from division in the basidium to division of the fusion nucleus in the probasidium, from pleurogenous spore formation to acrogenous, and finally from 4- to manysporedness, with fusions taking place between compatible basidiospores.

The second line of evolution within the Ustilaginales is towards the reduction of the basidium and a decrease in the number of spores. In this series the reduction of the basidium seems to be the consequence of plasmogamy between adjacent cells whereby both meiosis and dikaryotization have been compressed into the single organ and this has led to its degeneration. Thus in Ustilago Scabiosae and in many other species, the spores are freed before conjugation, whereas in Cintractia Montagnei (Fig. 4) there are fusions between the adjacent cells by means of clamp connections, and on each of the two clamps a single basidiospore is formed into which pass the + and — nuclei. Although as a result of this method of dikaryotization the spores are equipped with nuclei of opposite sex potentialities and are able to reproduce the species after infecting the host, nevertheless it is the first step in the reduction of the basidium since now it is only able to produce two spores and therefore is only the equivalent of a two-celled basidium. Ustilago nuda becomes more reduced since there is a delay in the formation of basidiospores after plasmogamy, but this reduction is carried by Ustilago longissima var. macrospora to a stage which simulates apogamy in which only one binucleate spore is formed at a time. The two nuclei of opposite sex factors are separated by a septum but these then come together by means of a clamp connection and pair, and the germ tube which is later formed produces sporidia that fuse normally. The last stage of reduction is reached in Sporobolomyces where there is apparently a complete loss of sex. Thus this line of evolution closely parallels that found in the Ascomycetes as illustrated by the Endomycetales-Saccharomycetales series postulated by Guillermond (1902), and apparently the same factors are involved.

## Tremellales—Autobasidiomycetes

Just as the Auriculariales and the Ustilaginales appear to have had their origin in the Uredinales, so too does it seem more than likely that the Tremellales trace back to the same source. The septate basidium immediately marks this order as relatively primitive, as does also the germination of the basidiospores by repeti-The best evidence for the manner in which the Tremellales originated is furnished by Weir (1912) who reported that not all the probasidia of Coleosporium Pulsatillae germinate to form transversely septate basidia, but that some of them germinate and become cruciately divided and thus are homologous with the basidium of the Tremellales. Hence if the spore-bearing projection from each cell of the transversely septate basidium is labelled a sterigma, then logically the same projections from the cruciately divided basidia must fall in the same category and the term epibasidium becomes superfluous. If the Tremellales are derived from an ancestral uredinaceous form that was characterized by a change from the stichobasidial orientation of the nucleus to the chiastobasidial, it may be assumed that these forms have become saprophytic during the passage of time and coincidently with this change there has been a great increase in gel production over that found in the coleosporiaceous ancestor. Just as in the Dacryomycetales and the Auriculariales, there are present in this group conidia which are at first binucleate and, although the spores may become uninucleate through subsequent septation, they may well represent a remnant of the habit of forming aeciospores.

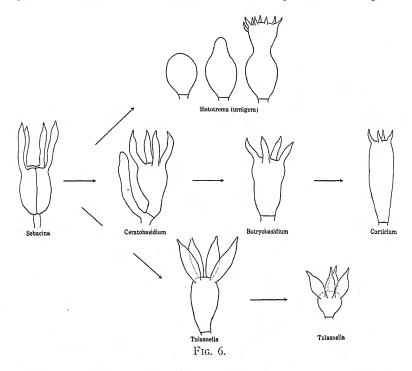
In thus deriving the Tremellales from the Coleosporeae, it would seem that the most primitive form would be pustulate. Since the basidiospores of *Tremella* produce sporidia closely resembling those of the rusts, it is considered the most primitive genus and *Exidia* with the sickle-shaped sporidia is derived from this genus.



From Tremella also, through the assumption of the resupinate habit of growth, comes Sebacina which in turn gives rise to three evolutionary lines: (1) Sebacina—Tremellodendron—Clavariopsis, (2) Sebacina—Heterochaete—Eichleriella—Protomerulius—Protohydnum—Tremellodon, (3) Sebacina—Tulasnella as shown in figure 5. The Sirobasidiaceae are derived from Tremella also and represent a line that has resulted from the basipetalous proliferation of basidia by the efficient utilization of the dikaryotic cells of the subtending mycelium. The position of the Hyaloriaceae is less obvious since the fructification is angiocarpous. However, it seems

that this monotypic family may be derived from a *Tremella*-like ancestor through the production of a more or less stromatic base surmounted by the hymenium which is penetrated by elongate, sterile, paraphysoid, gel secreting hyphae among which the basidia are scattered. In general, the evolutionary lines in this order follow closely those in other groups already discussed.

At this point it seems desirable to examine the Tulasnellaceae more carefully since much has been made of Tulasnella as a primitive genus among the Basidionycetes, and as a connecting link between some ascomycetous ancestor and the Autobasidiomycetes and the Tremellales. It appears that the Tulasnellaceae have received more attention in this connection than the family justly deserves. If the Tremellaceae are briefly surveyed, it will be found that within the family there is considerable variation in the septation of the basidium, both as regards to orientation and to number of septa (Coker 1920; Whelden 1934, 1935). Since one or two or even three of the longitudinal septa (Whelden 1935) may be lost, there should be no reason why all of the septa may not, and when this happens the resulting basidium is similar to that described by Rogers (1935) for Ceratobasidium or for Tulasnella (1932). Furthermore, if the survey is continued, it will be found that germination by repetition plays a very important rôle in the group. When the basidiospores germinate, they do so by producing one or more germ tubes, each of which produces one, or, according to Brefeld (1888), in the case of Exidia repanda more than one sporidium. When more than one sporidium is formed, it is obvious that there must be one or more divisions of the nucleus in the basidiospore. During the course of evolution, one of these divisions of the nuclei is advanced in time and place, coming to take place in the sterigmata. Whether or not this swelling of the sterigma to spore-like proportions is a result of nuclear activity or whether the swollen sterigmata in the past have served as a temporary resting point for those species which grew in cold weather or encountered drouths during the growing season, cannot satisfactorily be explained without more information in regard to the life history and biology of the forms. It is, however, significant that there is a transition to or from the conspicuously inflated sterigmata to the less inflated sterigmata characteristic of Ceratobasidium or to a non-septate tremellaceous basidium. It is also significant that the spore types exactly parallel those found on the one side in *Sebacina* and on the other, those found among the primitive members of the Corticiaceae. This parallelism of spore



types seems to indicate a definite relation between the Tulasnel-laceae and the other two groups and to suggest that it represents an end line that is intermediate between the Tremellaceae and Ceratobasidium in its origin, with those species characterized by conidium-like sterigmata representing the highest development. At all events, the basidium with the conidium-like sterigmata scarcely represents a primitive type derived from an ascus as Rogers (1932) intimates when he observes that "The sporoid characters of the Tulasnella epibasidium strongly suggest its evolution from the ascospores; consequently the epibasidium may be taken as the true homologue among the basidiomycetes of the ascospore, and the basidiospores as the homologues rather of an ascospore germination-conidium." So far as the writer is aware, there are no Asco-

mycetes in which the nuclei divide in the ascus in the same manner as do the nuclei of the Tremellaceae or Tulasnellaceae. The definitely chiastobasidial orientation near or somewhat below the apex of the tremellaceous basidium immediately characterizes the two basidiomycetous families and would appear to make impossible the derivation of tulasnellaceous basidium directly from an ascomycetous antecedent. For this reason it is more logical to look on the Tulasnellaceae as only secondarily derived from the Ascomycetes by way of the rusts and the Tremellales.

The Corticiaceae have been derived from the Tremellales in much the same manner as the Tulasnellaceae—by the loss of septation in the basidium. The transition, in this instance, is more clear-cut and direct since there are no secondary characters, such as are introduced by the inflated sterigmata, to obscure the relationship. As is shown in figure 6, the basidium of Ceratobasidium is essentially a mirror image of that of Sebacina, lacking only the internal septation. Furthermore the spores germinate by repetition and, as stated above, the spores show the same variation in morphology. For these various reasons, Ceratobasidium as described by Rogers (1935) therefore makes an ideal connecting genus almost exactly intermediate between the Sebacina-like ancestor and Botryobasidium. This latter genus also is in part characterized by a few species of which the basidiospores germinate by repetition, and differs from Ceratobasidium only in that the size of the sterigmata in proportion to the basidium is somewhat reduced. Through further reduction in the proportion of sterigmata to the basidium, and through elongation of the basidium itself, it is a simple matter to derive the Corticium-type of basidium which is found throughout the majority of the Corticiaceae, with the exception of those forms characterized by the Urnigera-type of basidium. This type appears to trace back directly to the tremellaceous basidium for in its early stage of development the probasidium is a subsphaerical body which then elongates by a relatively narrow neck that later expands and bears four to eight slender sterigmata around the apex. Before any final disposition in a phylogenetic scheme may be made, however, it would be best to know considerably more about the nuclear behavior of these forms. For the present it must suffice to hazard a guess as to its position and to point out that this type of basidium appears to be the basis of a definite line of evolution that leads into a number of the higher forms represented in the Hydnaceae and Polyporaceae, and in part shows an evolutionary history that runs side by side with the *Corticium*-type of basidium. Thus, within the Corticiaceae are developed the three main types of basidia to be found in the higher families of the class, and these must be taken into consideration in any discussion of their classification or phylogeny.

## SUMMARY

By excluding exceptional and isolated forms of the Basidiomycetes, it is possible to observe that there has been a general trend that has led from the Uredinales to the higher groups of the Basidiomycetes. This evolution has resulted from changes in lifecycles, from changes in time and position of nuclear divisions, and from changes in mode of living. It is possible to postulate that these variations have, to a great extent, resulted during geologic ages from slight differences in genetic characters that have been selected and perhaps continuously modified by environmental factors. As a result we are today dealing with forms, some of which have kept several primitive characters, but at the same time show others that are more advanced.

During the course of evolution of the Basidiomycetes, the haploid phase has become less and less important while the dikaryon stage has become dominant, and with this change, the process of spermatization has given way to plasmogamy. The basidium, once established, is essentially the same throughout the class but has undergone simplification as the result of loss of septation. Also, this same structure in the higher forms has taken over the functions of the probasidium so that it has become the locus of both caryogamy and meiosis. Because of the relatively gradual changes, and because of the essential unity in structure and function of this organ, the terminology relative to the basidium can be greatly reduced and a return may be made to the simple descriptive terms that were in vogue prior to the present age of ultra-refinement of definitions.

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## THREE NEW HYPHOMYCETES PREYING ON FREE-LIVING TERRICOLOUS NEMATODES

CHARLES DRECHSLER

(WITH 3 FIGURES)

In an earlier paper (8) was given a comparative account of 18 interrelated mucedinaceous fungi found to subsist habitually on nematodes that they capture by means of vegetative parts variously adapted for prehension. These fungi had come to light in agar cultures started from discolored rootlets or from other affected vegetable materials, and later often further planted with pinches of friable leaf mold. Similar cultures prepared as circumstances permitted during the last few years have revealed 3 additional mucedinaceous forms obviously belonging in the same series as those previously discussed, and like them observed subsisting by the capture of free-living terricolous eelworms. As the forms appear not to have been recorded hitherto in mycological literature, they are described herein as species new to science.

#### A SECOND SPECIES OF DACTYLELLA WITH CONSTRICTING RINGS

A fungus more similar to Dactylella bembicodes Drechsl. than to any other known predaceous form appeared in numerous maizemeal-agar plate cultures that, after serving in the isolation of various species of Pythium from diseased plant tissues, had received, in addition to material put on them originally, some pinches of friable leaf mold collected near Butternut, Wis., in September 1938. The mycelial hyphae of the mucedinous species in question invariably grew out from the deposits of forest detritus to ramify rather sparsely through the adjacent substratum. On the hyphae were borne at intervals three-celled predaceous rings closely resembling the constricting rings produced by D. bembicodes, Arthrobotrys dactyloides Drechsl., Dactylaria brochopaga Drechsl., and Trichothecium polybrochum Drechsl., the general similarity in cel-

lular make-up being clearly revealed in specimens jostled into nearly horizontal positions by passing nematodes (FIG. 1, A, a; B, a, b; C, a, b; D). In such positions the three component cells usually display a median thickening that bulges toward the center of the ring. As is evident even when the rings are examined in their normal positions at approximately right angles to the parent filament (FIG. 1, E; F; G, a; I, a, b; J, a), the supporting stalk here, while also consisting regularly of two cells, is perceptibly longer than in any of the four other species with constricting organs. The incidental difference in structural detail does not make for any difference in operation; for the rings of the present fungus, like those of the constricting species previously described, capture intruding nematodes by abrupt contraction and swelling of their component cells, which then send haustorial filaments into the interior of the disabled prey to appropriate its fleshy contents (FIG. 1, G, b; H; I, c; J, d). Likewise, as in the other constricting species, closed rings holding no prey are to be seen near captured animals, their closure having apparently resulted from proximity to captured eelworms (Fig. 1, J, b, c).

Since captured eelworms lash about violently in their efforts to free themselves, it is not unnatural to presume that the stimulus effective in the unprofitable closure of constricting rings within the orbit of their struggles may be one of mechanical irritation. instance of such closure incidentally shown in a figure of Dactylaria brochopaga (8: p. 515, fig. 13, D, e) was accordingly explained (8: p. 549) as having apparently been brought about by lashings from two specimens of *Diploscapter coronatus* (Cobb) Cobb that were found captured in rings nearby. Experimental evidence that a tactile stimulus is generally operative in closure of constricting rings has recently been supplied by Comandon and de Fonbrune (3, 4), who worked mainly with D. brochopaga and in lesser measure with Dactylella bembicodes. On gently irritating with a microneedle any one of the 3 arcuate cells on its inner or central side, they obtained motion pictures that recorded pronounced centripetal dilation of the irritated cell ensuing in the course of .1 second, followed a fraction of a second later by similar abrupt dilation of the other 2 cells; the intruding needle being thereupon found engaged so firmly that it could not easily be withdrawn. However, Couch (5), working with *D. bembicodes*, found that movement of a fine glass rod on the inner surface of the open predaceous ring resulted in only slight swelling, and concluded therefore that mechanical irritation plays a very small, if any, part in closure of the loops. Heat, whether supplied from a hot scalpel or in water having a temperature of 33° to 75° C., he found consistently effective in springing the traps; though, as was recognized by him, a thermal stimulus can hardly be postulated in the normal entrapment of cold-blooded animals.

The divergence between Couch's findings and those of Comandon and de Fonbrune suggests that further inquiry into the physiology of the constricting ring—assuredly one of the most remarkable of plant structures—might not be misdirected. Occasion may be taken to explain in this connection that for lack of a micromanipulator my own observations on the closure of the strangulating organs have been limited so far to three instances of capture; two of these instances having occurred in cultures of Arthrobotrys dactyloides, the other in a culture of Dactylaria brochopaga. The abrupt initial closure, whereby the animal was held fast, did not seem in these few instances to effect constriction in definitive measure. Appearances indicated rather that in the region where the captured nematode was encircled its body had been squeezed to approximately one-fourth of its normal compass, so that in the beginning musculature and organs, though rather severely compressed, were by no means severed. During a period of approximately 30 minutes further constriction appeared to ensue, bringing about injury to internal parts of the animal, and consequently causing its disablement. Strangulation of prey in constricting rings was therefore considered as taking place, in some measure, progressively. Since the heavy musculature, especially of the larger sturdier nematodes, might well offer appreciable resistance to compression until its tone has become impaired by excessive exertion, partly progressive strangulation may, indeed, not be wholly at variance with complete initial closure of the predaceous ring under experimental conditions where. in the absence of a sizeable, reluctantly yielding animal body, closure is unopposed.

In an earlier paper (6) I recorded my failure to see any adhesive substance present on the constricting rings of the four fungi

then known to produce such predaceous organs. Rather unexpectedly some evidence of a glutinous secretion was found in examining a culture of the fungus under consideration. A completely closed ring in which no nematode had been captured was found connected with the head of a living nematode by a delicate filament of an extremely elastic substance. The animal repeatedly stretched this filament to a length of approximately 10 µ, then being apparently unable to increase its pull, it held the filament under tension for a few seconds before relaxing. On cessation of the strain, the animal's head was promptly drawn back close to the swollen ring, through contraction of the elastic tether to a length of about 1 μ. After several seconds of rest the nematode again stretched its leash with the same futile outcome as before. The effort was repeated some hundreds of times in the course of an hour. The curious gynnastic exercise appeared of little significance, except in showing vividly that an elastic adhesive substance was somehow present on the inner surface of the ring. As adhesive material would seem superfluous for detaining eelworms caught in a swollen ring, it may conceivably function in ordinary instances of capture as part of the mechanism that springs the annular trap.

When amply provided with nourishment from captured nematodes, the mycelium of the fungus gives rise to scattered erect conidiophores, each bearing a single terminal conidium (FIG. 1, K, L, M). This asexual reproductive apparatus reveals morphological features distinctive of the species. While in all congeneric predaceous forms previously described the conidiophore tapers continuously from base to apex, in the present fungus it expands at the apex into a knob-like termination (FIG. 1, N, O). Contrary to expectations that might be entertained under the circumstances, attachment of the conidium to this distended apex (FIG. 1, K, L, M) is not appreciably wider than in related species where no terminal modification is present. After disarticulation of the conidium its base does not show the somewhat convexly rounded truncate outline usual in related forms, but commonly retains a noticeably concave profile with rather sharp demarcation between peripheral wall and basal membrane (Fig. 1, P, a-s, v). This aberrance in proximal outline of the asexual spore may possibly be traceable to a somewhat different manner of conidial abjunction

from that prevailing in other species; a close juxtaposition of two septa observable at the base of some spores (FIG. 1, P, t, u) suggesting that abjunction may be accomplished here through separation of two distinct partitions rather than by median splitting of a single partition. Some little encouragement for such an interpretation is supplied in the fact that the conidia regularly contain only two septa, which delimit a small basal cell and a small apical cell from a large ventricose median cell; whereas the conidia of similar conformation in Dactylella bembicodes and Dactylaria thaumasia Drechsl. regularly contain three septa, spaced so as to delimit two rather small cells below and a small apical cell above a large ventricose penultimate cell. It must be admitted, of course, that the presence of a concave basal outline in the three-septate conidia occasionally produced by the form under discussion (Fig. 1, P, v), and the absence of such an outline in occasional two-septate spores of D. bembicodes, D. thaumasia, and Arthrobotrys dactyloides, argue somewhat against the suggested interpretation.

Uniseptate conidia (FIG. 1, P, r, s) are somewhat more frequently observed in cultures of the fungus than triseptate specimens, though their maturity and even more the maturity of undersized conidia devoid of cross-walls (Fig. 1, P, q) is naturally subject to doubt. The biseptate condition, in any case, predominates so strongly that it must be considered characteristic of the species. With respect to their main dimensions the conidia show rather moderate ranges of variation. The relevant metric data included in the diagnosis were derived from 100 measurements of biseptate conidia selected at random in equal numbers from nematode-infested cultures and from pure cultures showing abundant sporulation. These measurements gave a distribution of values for length, expressed to the nearest micron, as follows: 28 µ, 2;  $29 \mu$ , 3;  $30\mu$ , 2;  $31 \mu$ , 3;  $32 \mu$ , 11;  $33 \mu$ , 19;  $34 \mu$ , 16;  $35 \mu$ , 21;  $36 \mu$ , 7; 37  $\mu$ , 11; 38  $\mu$ , 4; 39  $\mu$ , 1; and a distribution of values for width expressed to the nearest micron, as follows: 15  $\mu$ , 1; 16  $\mu$ , 1;  $17 \mu$ , 3;  $18 \mu$ , 9;  $19 \mu$ , 26;  $20 \mu$ , 31;  $21 \mu$ , 14;  $22 \mu$ , 11;  $23 \mu$ , 3;  $24 \mu, 1.$ 

After a conidiophore has served its primary function it frequently declines to the substratum, and gives rise, often from one of its basal cells, to a secondary conidiophore (FIG. 1, O) whereon

another conidium is borne. Instances of somewhat different repetitional development are found occasionally when conidia, after falling on a stale substratum, germinate by the production of a delicate, erect conidiophore (FIG. 1, Q) that in due course bears a secondary conidium.

On fresh agar media the conidia germinate promptly by the more commonplace production of germ hyphae, which readily grow out to form extensive mycelia. Pure cultures of the fungus, free of bacterial contamination, have been obtained conveniently by removing newly formed asexual spores from the tall hyphae supporting them, to tubes of sterile maizemeal agar; the removal being accomplished by means of slabs of a sterile agar medium held on a flamed platinum spatula. In these pure cultures tall conidiophores and biseptate ventricose conidia, much like those produced by predaceous mycelia, were always formed abundantly, often with a relatively small number of hyaline conidioid bodies apparently not corresponding to any structures hitherto observed in related species. Apparently the bodies in question are never borne on tall conidiophores of the same type as those bearing the ventricose conidia, but instead are produced singly on short, erect, slightly tapering, hyaline branches, often once or twice septate, and usually measuring 10 to 20  $\mu$  in length, 3  $\mu$  in width at the base, and about  $1.5 \mu$  in width at the apex (Fig. 1, R-U). They are mostly of a more or less cylindrical shape, bluntly rounded at the apex and usually tapering somewhat toward the basal end (Fig. 1, R-U; V, a-h). They commonly measure 20 to 40  $\mu$  in length and 6 to 8  $\mu$ in width. Although occasional specimens, presumably representing early stages of development, contain vacuolate protoplasm (FIG. 1, V, f) not markedly different from that of young conidia, most of the bodies (FIG. 1, V, a-e, g, h) are largely filled with globules of nearly uniform size that appear arranged in transverse layers somewhat like bullets in canister shot. Many of the bodies (FIG. 1, R; S; T; V, h), including especially the shorter ones, appear almost certainly to be continuous; others show vague indications of an approximately median septum (FIG. 1, U; V, a-e, g), though owing to the difficult optical conditions associated with the globulose internal structure I have so far not been able to satisfy myself that a cross-wall is actually present.

The production of the elongated spore-like bodies in addition to large ventricose conidia might possibly be considered expressive of a tendency toward dimorphism comparable yet opposite to the tendency toward conidial dimorphism in Arthrobotrys dactyloides; for with respect to dimensions and shape the bodies resemble the uniseptate elongated conidia usually produced by A. dactyloides, while the swollen biseptate conidia occasionally produced by that species are not dissimilar to the ventricose spores typical of the present fungus. However, in A. dactyloides the conidia of the more exceptional type are borne on the same tall conidiophores as those of the usual type, and the two types show no marked difference either in the organization of their contents or in their readiness to germinate. Any presumed analogy with A. dactyloides is thus seriously disturbed; and it remains very uncertain whether the elongated bodies can be at all closely homologized with the ventricose conidia.

Of the several morphological features that might suggest a suitable epithet for the species, the bulbous apical modification of the conidiophore appears least apt to convey an objectionable connotation. At the risk, perhaps, of some exaggeration the fungus is described under a name compounded of two words meaning "pestle" and "form" respectively.

# Dactylella doedycoides sp. nov.

Mycelium effusum; hyphis hyalinis, septatis, plerumque 2-4 \(\mu\) crassis, laqueos circulares 20-36 \mu latos in 3 cellulis arcuatis 16-28 \mu longis medio 4-7  $\mu$ , extremo 2.5-5  $\mu$  crassis consistentes ex ramulo biloculari circa 10-20  $\mu$ longo 2.5-4 \( \mu\) crasso proferentibus; his laqueis vermiculos nematodeos illaqueantibus, deinde tum per contractionem et inflationem trium cellularum animalia magnopere comprimentibus, ita haec trucidentibus, statim integumentum perforantibus, hyphas intus evolventibus quae carnem exhauriunt. Hyphae fertiles hyalinae, erectae, septatae, plerumque 225-500 \( \mu \) altae, basi 5-8 μ crassae, sursum leviter attenuatae, prope apicem 2-3 μ crassae, apice abrupte tuberantes, ibi 3-5 μ crassae et unicum conidium ferentes. Conidia hyalina, turbinea, apice rotundata, deorsum paulum attenuata, basi abrupte truncata vel saepe aliquantulum cavata, 28-39 \mu (saepe circa 34 \mu) longa, 15-24 μ (saepe circa 20 μ) lata, vulgo biseptata—loculo infimo obconico, 4-10 μ (saepe circa 6.6 μ) longo; loculo medio dolioformi, ventricoso, 16-26 μ (saepe circa 22.7  $\mu$ ) longo; loculo summo 2.5-7  $\mu$  (saepe circa 4.7  $\mu$ ) longo. Vermiculos nematodeos multarum specierum usque .6 mm. longos laqueans

Mycelium spreading; vegetative hyphae hyaline, septate, mostly

consumensque habitat in humo silvestri prope Butternut, Wisconsin.

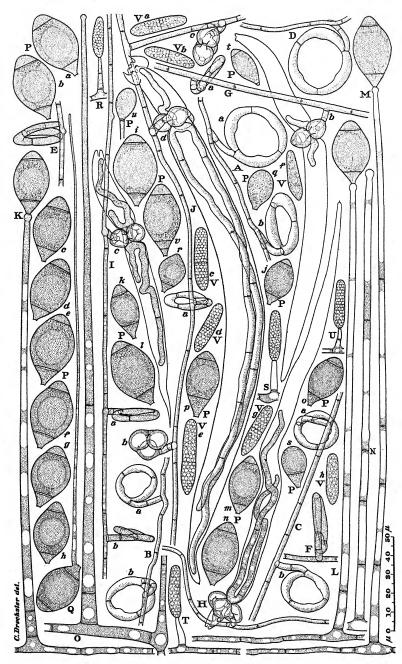


Fig. 1. Dactylella doedycoides.

2 to 4  $\mu$  wide, often, especially in the presence of nematodes, producing mostly underneath and at right angles to their axes approximately circular rings 20 to 36 µ in outside diameter, composed individually of 3 arcuate cells 16 to 28  $\mu$  long, 4 to 7  $\mu$  wide in the middle, and 2.5 to  $5 \mu$  wide at the ends—the first and third of the cells being united usually to each other as well as to the distal end of a somewhat curved or straight supporting branch 10 to 20 u long, 2.5 to 4 \u03c4 wide, and consisting usually of 2 cells; following ensnarement of a nematode the individual ring through contraction and inflation of its component arcuate cells constricting the animal to death or into a state of reduced activity preceding death, then perforating the integument and extending lengthwise through the body assimilative hyphae that appropriate the fleshy contents. Conidiophores hyaline, erect, septate, 225 to 500 \( \mu \) high, 5 to 8 \( \mu \) wide at the base, tapering gradually upward to a diameter of 2 to  $3 \mu$ , then expanding abruptly into a knob-like tip 3 to  $5 \mu$  wide, whereon is borne a single conidium. Conidia hyaline, somewhat top-shaped, often tapering noticeably toward the abruptly or somewhat concavely truncate base, 28 to 39  $\mu$  (average 34  $\mu$ ) long, 15 to  $24 \mu$  (average  $20 \mu$ ) wide, usually divided by 2 septa into 3 cells—the basal obconical cell then measuring 4 to 10 µ (average  $6.6 \mu$ ) in length, the middle swollen barrel-shaped cell measuring 16 to 26  $\mu$  (average 22.7  $\mu$ ) in length, and the terminal cell measuring 2.5 to  $7 \mu$  (average  $4.7 \mu$ ) in length.

Capturing and consuming nematodes measuring up to .6 mm. in length, referable to such genera as *Aphelenchoides*, *Plectus*, *Rhabditis*, *Diploscapter* and *Wilsonema*, it occurs abundantly in leaf mold in deciduous woods near Butternut, Wis.

## A SPECIES OF DACTYLARIA WITH STALKED ADHESIVE KNOBS

Among several cultures of nematode-capturing fungi that Dr. M. B. Linford (12) isolated from Hawaiian soils and very kindly sent to me late in 1937 was a species of *Dactylaria* conspicuously different from any of the similarly predaceous hyphomycetous forms with which I had at the time become acquainted. Although the species had not been seen in the many cultures prepared, as occasion offered during the preceding four years, mainly with decaying vegetable refuse collected near Washington, D. C., it appeared in May, 1938, in a number of *Pythium* cultures to which had been added small pinches of somewhat woody, friable remnants from rotting stems of the giant ragweed, *Ambrosia trifida* 

L., collected in Arlington, Va., a few weeks earlier. Addition of the ragweed detritus afforded development of bacteria in such meager quantity that nematodes addicted to ingestion of bacterial slime multiplied only sparingly, while forms equipped with a stylet and subsisting on protoplasm sucked from living Pythium filaments attained appreciably greater numbers. By far the most numerous of the eelworms expropriating the oomycetous mycelium was a species apparently identifiable as Aphelenchoides parietinus (Bastian 1865) Steiner 1932, whose frequent parasitism on fungus hyphae has been set forth by Christie and Arndt (2). Because of its abundance this species provided the chief source of nourishment for the new Dactylaria, which, wherever observed, was always found to have extended its mycelium from a deposit of ragweed refuse into the surrounding agar substratum. Other nematodes. including representatives of the genus Rhabditis, were also utilized by the fungus, suggesting that its development in the cultures was perhaps encouraged more by the relative freedom of the substratum from growth of putrefactive bacteria than by the taxonomic relationships of the eelworms available for consumption.

Although the new species of *Dactylaria* is correctly to be reckoned among the predaceous fungi, its attack on nematodes in my cultures was for the most part that of a parasite; for in most instances the animals were invaded by germ-tubes from adhering conidia. Usually several conidia were found attached to the anterior end of a nematode undergoing infection, so that as the encumbered animal continued to move about it gave somewhat the appearance of being provided with excessively long cephalic processes (FIG. 2, A). Infection was accomplished by narrow perforation of the integument, and extension into the animal of a germ tube from each conidium. The germ tubes continued their growth lengthwise through the nematode as branching hyphae, their advance being marked by fatty degeneration of musculature and internal organs. After appropriating the degenerating materials the internal hyphae would break through the integument and extend themselves into the surrounding substratum as new mycelial filaments on which would be borne at intervals stalked globose knobs (FIG. 2, B-G) generally similar to the predaceous knobs of Dactylella ellipsospora Grove and D. asthenopaga Drechsl. Much

as in these two species the globose knobs were functional in the capture of prey by means of a transparent adhesive substance secreted by them. A process arising from the individual knob would grow through the cushion of adhesive substance, narrowly perforate the animal's integument, and intrude a subspherical body that would disable the animal, thereby rendering it subject to invasion and expropriation by haustorial filaments.

With ample nourishment being supplied by captured animals, the fungus produces erect conidiophores that are shorter and more delicate than those of any other hyphomycetous form now known to prey on nematodes. Following development of a first conidium (FIG. 2, H) the axis of the conidiophore often elongates to produce a second one farther on, the first being pushed into a lateral position. Repetition of the process results in the development of several conidia in a loosely radiating head. The conidia are relatively uniform in structural design (FIG. 2, N, a-z; O, a-z; P), in nearly all instances being divided by four transverse septa into five cells. Four of these cells, approximately cylindrical in shape and nearly equal to one another in length, make up the main part of the spore. The fifth cell terminating the conidium is of a prolate ellipsoidal shape like the predaceous knobs borne on the mycelial hyphae. Though noticeably smaller than those knobs, it is nevertheless similarly adhesive, and functions in attaching the conidium to any active eelworm that may chance to come in contact with it. Occasionally a second adhesive knob may be found present at the proximal end of a detached spore (Fig. 2, O, a, l, p); its development possibly having taken place subsequent to disarticulation. Now and then a conidium may contain as many as eight cylindrical segments (FIG. 2, O, k), following division of some or all of the four cylindrical segments ordinarily present by median septa.

On removing its conidia from the conidiophores to sterile agar media by means of a small agar slab held on a flamed platinum spatula, the fungus may often be brought directly into pure culture, though at times further procedure may be necessary to remove contaminating bacteria. Even in the absence of extraneous organisms the mycelium is extended rather slowly on maizemeal agar, and when extended, is usually somewhat inconspicuous, owing

to meager development of aerial elements. Besides the hyphal anastomoses frequent in related species, the fungus shows in pure culture scattered knots composed of irregular hyphal branches intricated with one another. Sporulation is usually somewhat tardy, yet after several weeks numerous conidiophores are often present, many of them bearing individually 10 to 15 conidia in loose capitate arrangement (FIG. 2, I, I) on a sporiferous tip modified with slight geniculations and an occasional spur (FIG. 2, K, L, M). The conidia thus produced, like those found in nematode-infested cultures, are always provided distally with a globose adhesive knob.

In no other fungus so far known to prey on nematodes is the conidium consistently furnished with a special adhesive part at the time of its development. The nearest approach to such consistent modification is shown in *Dactylella leptospora* Drechsl., which often in pure culture and occasionally in nematode-infested cultures gives rise to conidia bearing terminally a globose knob. In *D. leptospora*, it is true, the conidial knobs have not been seen operative in attaching spores to active eelworms; whereas in the fungus under consideration the homologous modifications are conspicuously efficient in promoting a parasitic mode of attack. Presumably, however, this marked difference in observed usefulness derives from a difference in suitableness of some agar substrata for the operation of the conidial knobs produced by the two species, rather than from any essential difference in function.

A term compounded of two words meaning "to fasten" and "seed" respectively, is deemed an appropriate specific epithet for the fungus.

## Dactylaria haptospora sp. nov.

Mycelium effusum; hyphis sterilibus septatis, hyalinis,  $1.3-4.5\,\mu$  crassis, bullas globosas vel ellipsoideas  $6-10\,\mu$  longas,  $5-8.5\,\mu$  crassas, ex ramulo recto vel curvato, saepius  $4-30\,\mu$  longo, circa  $1.5-2.5\,\mu$  crasso, continuo vel 1-3-septato emittentibus; his bullis ad vermiculos nematodeos inhaerentibus, ita animalia tenentibus, integumentum eorum perforantibus, hyphas intrudentibus quae carnem exhauriunt. Hyphae fertiles hyalinae, erectae, septatae,  $50-150\,\mu$  altae, basi  $1.7-2.7\,\mu$  crassae, sursum leviter attenuatae, apice circa  $1.5\,\mu$  crassae, ibi plus minusve geniculatae interdum parce ramosae, 1-15 conidia in capitulum laxum singulatim deinceps gerentes. Conidia hyalina, elongato-cylindrata, in toto  $35-60\,\mu$  longa, medio  $2.2-3.2\,\mu$  crassa, vulgo in 5 cellulis consistentia: cellula summa globosa vel ellipsoidea,  $3-5\,\mu$  longa,

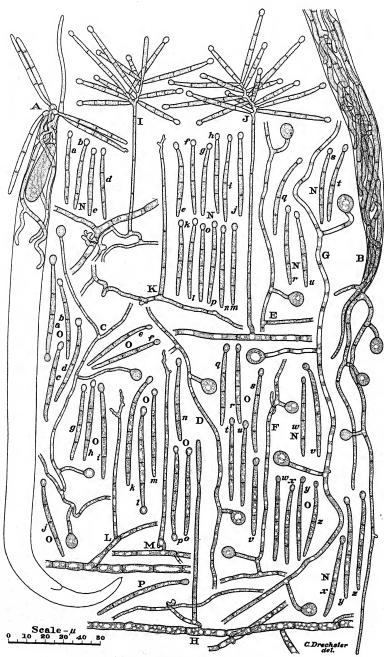


Fig. 2. Dactylaria haptospora.

 $2.5-3.7~\mu$  crassa, glutinosa itaque saepe ad vermiculos nematodeos inhaerente; 4 alteris cellulis inter se subaequalibus, conjunctim partem cylindratam saepius sursum et deorsum plus minusve attenuatam conficientibus. Conidia rarius 5-8-septata, atque rarius non modo apice sed etiam basi cellula glutinosa instructa.

Vermiculos nematodeos diversos interficiens habitat in caulibus putrescentibus Ambrosiae trifidae in Arlington, Virginia, item in terra agresti in Hawaii.

Mycelium spreading; the vegetative hyphae hyaline, septate, 1.3 to 4.5  $\mu$  wide, often, especially in the presence of nematodes, giving rise here and there on stalks frequently straight or somewhat curved, 4 to 30  $\mu$  long, 1.5 to 2.5  $\mu$  wide, continuous or containing 1 to 3 septa, to unicellular adhesive knobs subspherical or prolate ellipsoidal in shape, 6 to 10 \u03c4 long and 5 to 8.5 \u03c4 wide; the knobs holding fast to nematodes, individually perforating the integument of the adhering animal, and intruding haustorial filaments lengthwise through its body to appropriate the fleshy contents. Conidiophores hyaline, erect, septate, 50 to  $150 \mu$  high, 1.7 to  $2.7 \mu$  wide at the base, very gradually tapering upward to a width of about 1.5  $\mu$ , then terminating often in a slightly branched more or less geniculate sporiferous part formed by repeated elongation following successive apical production of conidia up to 15 in number in loosely capitate arrangement. Conidia hyaline, elongated cylindrical, 35 to  $60 \mu$  long, 2.2 to  $3.2 \mu$  wide in the middle, usually divided by 4 septa into 5 cells: the distal cell globose or prolate ellipsoidal, 3 to  $5 \mu$  long, 2.5 to  $3.7 \mu$  wide, often adhering to a nematode and directly operative in causing its infection; the other 4 cells approximately equal to one another in length, together making up an elongated part often tapering more or less both toward its base and toward the tip. Conidia more rarely containing 5 to 8 cross-walls, and more rarely, too, provided with an adhesive globose cell not only at the apical end but also at the basal end.

Destroying various species of nematodes it occurs in decaying woody remnants of *Ambrosia trifida* in Arlington, Va., and also in field soils in Hawaii.

### A SPECIES OF TRIDENTARIA PREYING ON WEAKENED EELWORMS

A fungus of unusual predaceous behavior made its appearance in a maizemeal-agar plate culture originally used in isolating a species of *Pythium* from some discolored roots of a smartweed (*Persicaria Hydropiper* L.) plant dug up in a moist field near

Butternut, Wis., early in September, 1938. When the culture was several days old and completely permeated with *Pythium* mycelium, it had been further planted with pinches of leaf mold taken from deciduous woods near Butternut, Wis., early in September, 1938. Thirty days after this final addition of vegetable material a tract of the substratum embracing about 100 square millimeters and adjacent to one of the leaf-mold deposits was found sparsely permeated by a delicate septate mycelium reminiscent of the sparse mycelium of *Triposporina aphanopaga* Drechsl. The fungus had evidently grown out from the forest refuse, and seemed to be wholly dependent for nourishment on the nematodes captured by it.

Destruction of nematodes by the fungus was on a relatively small scale; the number of animals consumed altogether probably not exceeding five hundred. All of the eelworms examined soon after their capture, before their morphological features had become obliterated beyond recognition, appeared to belong to a single species tentatively identified as Aphelenchoides parietinus. The captives, whether large or small, invariably showed rather extensive infection, especially in their median and posterior parts, by an organism producing aggregations of subspherical spore-like bodies about  $1.5 \mu$  in diameter, each containing a somewhat eccentrically placed refractive globule approximately .6 µ in diameter. Continued accumulation of these minute bodies, which in shape and structure appeared closely comparable to some of the spores observed in nematodes by Micoletzky (13: p. 285-286, Taf. XI, 49 c; 50 c, d), was accompanied by progressive enfeeblement and finally complete disablement of the animal. Only nematodes already much enfeebled by the internal parasite were taken by the fungus.

This limitation in predaceous activity has its cause apparently in the meager differentiation of the mycelial elements operative in effecting capture. Repeated examination failed to disclose any evidence that vegetative filaments ever give rise to structures recognizable as predaceous apparatus previous to the moment prey is engaged and held; though, to be sure, captured nematodes are usually found encircled by a hyphal branch (FIG. 3, A–D) in a manner recalling the encirclement of eelworms by non-constricting rings of  $Dactylella\ leptospora\ and\ Dactylaria\ candida\ (Nees)$ 

Sacc. In some instances the encircling element may even constitute a ring with a closure of contact if not of anastomosis (FIG. 3. A). More frequently, however, the tip of the element is definitely free, and the impression given is that encirclement came about through growth of the branch around the animal after its capture (FIG. 3, B; C; D, c, d). Unless appearances are misleading the animal is held at the beginning merely by adhesion to the distal part of a hyphal branch. If the branch is not already wider than the parent mycelial filament, it undergoes some widening subsequently, either throughout its length, or at times more especially in its distal portion. As the thickened branch continues its growth somewhat laterally in giving rise to the encircling element, its adhering tip narrowly perforates the integument of the captive and sends haustorial hyphae lengthwise through the fleshy interior. Some nematodes (FIG. 3, D, b) are captured and encircled by two separate branches (FIG. 3, D, c, d); and, again, a branch (FIG. 3, D, c) after participating in the capture of one eelworm (FIG. 1, D, b) may continue growth and capture a second (Fig. 1, D, a). Development of haustorial filaments is very often noticeably less abundant than in nematodes preyed upon by other hyphomycetes the more meager development having an obvious explanation in the partial appropriation of available materials by the minute parasite.

Conidiophores were found arising here and there from the tract of mycelium (Fig. 3, E–J). In stature they show closest similarity to the fertile hyphae of Dactylella tenuis Drechsl. The conidia (Fig. 3, K, a–z, L) produced on them singly are of unusually distinctive make-up, being composed as a rule of a short obconical two-celled basal part together with three digitate or pronglike distal parts, each of which is divided by three to five transverse septa into four to six cells. In number of conidial prongs the fungus at once recalls  $Tridentaria\ carnivora\ Drechsl.$ , a member of the predaceous series that was described in an earlier paper (9) as subsisting by the capture of the testaceous rhizopod  $Difflugia\ constricta\ (Ehrenb.)$  Leidy. However the relationship of the prongs to the basal part is different in the two species; for in  $T.\ carnivora\$ the basal part is prolonged directly into one of the prongs, whereas in the present species it bears all three prongs

alike as terminal branches in isogonal arrangement. Accordingly, while the conidia typical of *T. carnivora* are symmetrical with reference to only one plane, those of the present species are symmetrical with reference to three planes.

The isogonal branching evident in conidia of the fungus under consideration is more closely approximated in the tridental conidia (7: p. 396, fig. 1, Q, R) occasionally produced by Pedilospora dactylopaga Drechsl., a hyphomycetous form which I first described as predaceous only on the testaceous soil rhizopods Dif-flugia globulosa Duj. and Trinema enchelys Ehrenb., but which I have since found preying also on Sphenoderis dentata Pen. (10: p. 405–406) and Geococcus vulgaris Francé. Similarity in angular relationships is likewise apparent when the symmetrically two-pronged conidia typical of P. dactylopaga are compared with the two-pronged conidia (Fig. 3, K, f, z) produced occasionally by the present fungus. The symmetrical dichotomy in the bidentate conidia of both these forms is readily distinguished from the monopodial branching evident in the bidentate conidia produced now and then by Tridentaria carnivora (9: p. 392, fig. 1, I).

Germination of the curiously designed asexual spores takes place by the production of germ-tubes from the basal end and from the tips of the prongs (FIG. 3, M). As in other members of the predaceous series of hyphomycetes, anastomoses of fallen conidia with mycelial hyphae occur frequently (FIG. 3, N).

The fungus is referred to *Tridentaria* Preuss, a genus so poorly defined by its author (14) that misgivings as to the wisdom of retaining it have been expressed (11). When earlier I nevertheless ventured to commit *T. carnivora* to this little esteemed taxonomic repository, I was persuaded as much by the realistic appropriateness of the generic term invented by Preuss as by the sketchy definition presumably intended to govern its application. The term appears, if anything, even more felicitous in relation to the conidium of the present species, especially when this structure is considered in combination with the supporting conidiophore. A word meaning "encircling," which it is hoped may prove conveniently suggestive of the unusual predaceous behavior of the fungus, is proposed as a suitable specific name.

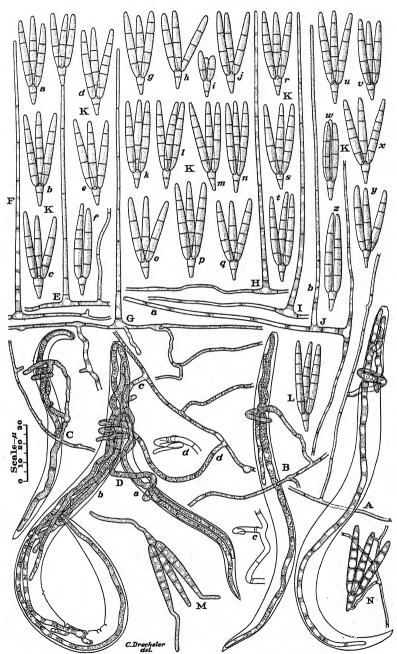


Fig. 3. Tridentaria implicans.

## Tridentaria implicans sp. nov.

Mycelium sparsum; hyphis sterilibus hyalinis, parce ramosis, mediocriter septatis, vulgo 1–2.5  $\mu$  crassis, ramos saepius 15–75  $\mu$  longos, 2–3.5  $\mu$  crassos gerentibus—his crassioribus ramis vermiculos nematodeos attingentibus et haerendo tenentibus, animalia implicantibus, integumentum eorum perforantibus, hyphas usque 4  $\mu$  crassas intrudentibus quae carnem exhauriunt. Hyphae fertiles erectae, hyalinae, septatae, simplices, 100–200  $\mu$  altae, basi circa 3.5  $\mu$  crassae, sursum leviter attenuatae, apice circa 1.5  $\mu$  crassae, unicum conidium ferentes. Conidia hyalina, raro bifurca in modum conidiorum generis Pedilosporae, vulgo ex 4 partibus ad instar fuscinae composita—parte infera quae hastile fuscinae facit obconica, uniseptata, basi 1–1.5  $\mu$  crassa, sursum latescente, apice rotundata, 4–5.5  $\mu$  crassa, ibi 3 dentes aliquantulum divaricatos ferente; dentibus digitiformibus, 12–42  $\mu$  saepissime 30–40  $\mu$  longis, 3.5–5  $\mu$  crassis, plerumque 3–5-septatis, basi rotundatis, sursum nonnihil attenuatis.

Vermiçulos nematodeos debilitatos capiens consumensque habitat in humo silvestri prope Butternut, Wisconsin.

Mycelium in mixed culture on agar substrata rather meager; vegetative hyphae hyaline, sparingly branched, septate at moderate intervals, commonly 1 to  $2.5 \mu$  wide, giving rise here and there to slightly differentiated branches often 15 to 75  $\mu$  long and 2 to 3.5  $\mu$ wide; these branches capturing nematodes by adhesion, then individually continuing growth to encircle the captive in 1 to 1.5 turns while narrowly perforating its integument and extending lengthwise through its interior assimilative hyphae up to  $4 \mu$  wide that appropriate the fleshy contents. Conidiophores erect, hyaline, septate, simple, 100 to 200  $\mu$  high, usually about 3.5  $\mu$  wide at the base. tapering gradually upward to a width of  $1.5 \mu$  at the tip, and there bearing a single conidium. Conidia hyaline, now and then bifurcate in the manner typical for conidia of the genus Pedilospora. but usually composed of 4 parts in trident-like arrangement—the basal part corresponding to the shaft of a trident being obconical, transversely uniseptate, 1 to  $1.5 \mu$  wide at the base, widening upward to a diameter of 4 to  $5.5 \mu$  at the bluntly rounded apex whereon are borne in isogonal arrangement the other 3 slightly divergent digitate parts corresponding to prongs of a trident: the prong-like parts 12 to 42  $\mu$  (usually 30 to 40  $\mu$ ) long, 3.5 to 5  $\mu$ wide, individually tapering noticeably upward from a broadly rounded basal end, and divided by 3 to 5 transverse septa into 4 to 6 cells.

Capturing and subsisting on weakened nematodes it occurs in leaf mold of deciduous woods near Butternut, Wis.

# CORRECTIONS CONCERNING DACTYLARIA BROCHOPAGA AND ARTHROBOTRYS SUPERBA CORDA

An incidental comment in a recent review (1: lines 20, 21) calls attention to an error of more than ordinary seriousness in my earlier paper on nematode-capturing hyphomycetes. The species which I intended to name Dactylaria brochopaga, and to which I referred in all other connections by that binomial, was, owing to a lapse of the pen, presented in its formal diagnosis under the binomial Dactylella brochopaga (8: p. 517, line 7). Despite the unhappy lapsus calami the species has fortunately been cited under its correct generic name by Comandon and de Fonbrune (3, 4), as well as by Roubaud and Deschiens (15). It is hoped that the binomial Dactylaria brochopaga will continue to be used in all future references to the fungus.

Rather curiously the somewhat troublesome similarity in spelling between the generic names Dactylaria and Dactylella is associated with an equally troublesome morphological intergradation between those members of the two genera that constitute members of the predaceous series. When developing on natural or on nematode-infested agar media, the fungi in question offer little difficulty, since on these materials their conidiophores ordinarily bear either a solitary terminal conidium or a terminal cluster of conidia. generic difference tends to become more or less obliterated when some of the fungi are grown in pure culture on agar media; for a number of capitate forms, including Dactylaria brochopaga, then often produce their plural conidia in extended arrangement, and certain forms more usually seen with solitary conidia, as, for example, Dactylella spermatophaga Drechsl., then likewise often produce plural conidia in extended arrangement on a conidiophore successively prolonged. On the other hand, two capitate forms, namely Dactylaria thaumasia and Dactylaria haptospora Drechsl., often appear somewhat more pronouncedly capitate when grown in pure culture, owing to a more copious production of conidia.

In my earlier paper, too, similarity of spelling facilitated an error (8: p. 454, line 28) resulting in a rather obvious misstatement concerning the conidia of *Arthrobotrys superba*. This mis-

statement is to be remedied by substituting for the unintended "uniseptate" the correct word "unseptate."

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## EXPLANATION OF FIGURES

Fig. 1. Dactylella doedycoides; drawn to a uniform magnification with the aid of a camera lucida; × 500 throughout. A, B, C, Portions of mycelial hyphae, each bearing two open constricting rings, a and b, that have been jostled by passing nematodes from their original approximately vertical positions into more nearly horizontal positions where their cellular make-up is better revealed. D, Portion of a mycelial hypha bearing an unusually large open predaceous ring that has been jostled into a nearly horizontal position. E, F, Portions of mycelial hyphae, each bearing an open predaceous ring apparently in its original position. G. Portion of mycelial hypha bearing two predaceous rings, one of them, a, being shown open, the other, b, having strangled a small nematode possibly identifiable as a larva of Aphelenchoides parietinus, and intruded into the captive two short haustorial branches. H, Portion of mycelial hypha bearing a predaceous ring that has strangled a nematode possibly referable to Plectus parvus Bastian, and extended two haustorial filaments through half the length of the animal. I. Portion of mycelial hypha bearing two open predaceous rings, a, b, apparently in their original positions, and a third ring, c, that after capturing and strangling a small specimen of Rhabditis dolichura Schneider has invaded the captive by means of four haustorial filaments. J, Portion of mycelium bearing one open predaceous ring, a, two predaceous rings, b, c, that have closed without capturing prey, and a fourth ring, d, that after strangling an eelworm probably referable to Wilsonema sp., has extended haustorial hyphae throughout the length of the captive. K, L, M, Portions of hypha, each with an erect conidiophore whereon is borne a mature conidium. N. Conidiophore denuded of the conidium it produced. O, A denuded conidiophore that was produced from the basal portion of an older one, which now is in contact with the substratum. P, Conidia:  $\alpha-p$ , mature specimens of usual type with two septa and more or less concave basal end; q, non-septate specimen that probably became detached while still immature; r, s, small specimens, apparently mature, though containing only one septum; t, small specimen with two septa, the proximal being so close to the convex basal end that it may possibly correspond to the usual basal membrane; u, young specimen set off from the sporophore by two septa very close together, the upper one possibly corresponding to the usual basal membrane, the lower one possibly corresponding to the basal membrane in exceptional specimens such as t; v, large mature specimen with septation unusual for the species, the three cross-walls showing the positional arrangement most frequent in conidia of Dactylella bembicodes and Dactylaria thaumasia. Q, Conidium germinating by production of a delicate erect germ sporangiophore. R-U, Short erect sporophores, each bearing an elongate spore that shows globulose internal structure and apparently is not homologous to a conidium. V, a-h, Elongate spores detached from erect sporophores, all of them except the apparently immature specimen f, showing characteristic globulose internal structure.

Fig. 2. Dactylaria haptospora; drawn to a uniform magnification with the aid of a camera lucida; × 500 throughout. A, Specimen of Aphelenchoides parietimus invaded at its anterior end by infection hyphae coming from five conidia adhering to the head; one of the conidia having apparently

germinated before becoming attached to the animal. (The oblong body shown in the nematode is a young thallus of the phycomycetous parasite Haptoglossa heterospora Drechsl.) B, Portion of a specimen of A. parictinus permeated with mycelium of the fungus; from the tail-end of the animal have grown out a few vegetative hyphae whereon are borne three stalked adhesive knobs. C, Portion of mycelium with four adhesive knobs. D, E, F, Portions of mycelium, each bearing two stalked predaceous knobs. G, Portion of hypha with four stalked predaceous knobs. H, Portion of mycelium with an erect conidiophore, which terminates in an immature conidium, the first to be produced by it. I, Portion of mycelium with an erect conidiophore on which are borne 11 mature conidia, a twelfth conidium being in process of development. J, Portion of hypha from which has arisen an erect conidiophore bearing 15 mature conidia. K, L, M, Portions of mycelium, each bearing a denuded conidiophore. N, a-z, O, a-z, P, Conidia showing variations in shape, dimensions, septation and number of adhesive organs.

Fig. 3. Tridentaria implicans; drawn to a uniform magnification with the aid of a camera lucida;  $\times$  500 throughout. A, B, C, Nematodes, possibly referable to Aphelenchoides parietinus, that after being weakened through extensive infection by a minute internal parasite, were captured individually by adhesion to a branch of the fungus, entwined by a hyphal prolongation, and invaded by haustorial filaments. D, Portion of mycelium with two captured nematodes a, b-nematode a having been captured, enveloped, and invaded by the distal part of branch c; while nematode b was captured, enveloped, and invaded conjointly by the branches c and d; the portions of branches c and d enveloping nematode b being also shown separately for clearness. E, Portion of hypha with an erect conidiophore on which a conidium is borne. F-I, Portions of mycelium, each with an erect denuded conidiophore. J, Portion of a hypha on which was produced a conidiophore, a, that after serving its primary function, declined to the substratum and gave rise to a secondary conidiophore. K,  $\alpha$ -z, L, Conidia showing variations in number and dimensions of shaft and prongs, and in abundance of septa. M, Conidium germinating by production of germ tubes from base of shaft and from tips of two prongs. N, Conidium anastomosing with branches of a vegetative hypha.

# NUCLEAR MIGRATION IN GELASINOSPORA

ELEANOR SILVER DOWDING AND A. H. REGINALD BULLER (WITH 6 FIGURES)

#### I. INTRODUCTION

In 1931, the senior author (Buller) discovered that, in *Coprinus lagopus*, during the initiation of the sexual process, nuclei migrate from one mycelium into another (1). Using two haploid mycelia of opposite sex, (AB) and (ab), he showed that a large mat of the mycelium (AB) could be diploidised by a small inoculum of mycelium (ab), so that all the growing hyphae of (AB) produced clamp-connexions (indicating the presence of conjugate pairs of nuclei); and he also showed that the rate of migration of the (ab) nuclei through the mycelium (AB) was about ten times the rate of elongation of the hyphae.

In 1933, Craigie (4) showed that, in the Uredinales, the union of a pycnidiospore with a flexuous hypha of opposite sex leads to the diploidisation of the haploid proto-aecidia, with the result that the proto-aecidia develop into aecidia. It is obvious that, after a pycnidiospore has united with a flexuous hypha of opposite sex, the nucleus of the pycnidiospore must migrate down the flexuous hypha, through the wall of the pycnidium, and through the vegetative intercellular mycelium in the leaf to the proto-aecidia. That nuclear migration through a mycelium takes place in the Uredinales may therefore be regarded as having been established.

In 1935, nuclear migration in the Ascomycetes was demonstrated by Dodge (5). He placed two mycelia of Neurospora tetrasperma, S3 and S9, which were of opposite sex, on opposite sides of an agar plate. Perithecia began to form as usual about the fourth day on the S9 mycelium on one side of the line of meeting. Four small blocks of agar bearing a very few young perithecia were then transferred to separate plates which were incubated for twelve hours. The hyphae of the mycelium in the blocks grew out so that single hyphal tips could be isolated very easily. Seven 1-tip

tube cultures were obtained from each of the four transplants. Later they all produced perithecia, which showed that the single tips isolated must have carried both kinds of nuclei. Said Dodge: "Since mycelia S3 and S9 with which the plate was inoculated are both unisexual, the bisexual tips isolated later from the S9 side must have represented new branches that grew out from the old S9 mycelium after it had received the S3 nuclei passed along down following anastomoses at the line of meeting." Dodge made similar experiments with Gelasinospora tetrasperma.

Some new experiments on nuclear migration in Gelasinospora tetrasperma will now be described. They were designed with a view to demonstrating once again the fact of nuclear migration in a multicellular mycelium and to solving problems concerned with: (1) the speed of nuclear migration; (2) the effect of light on nuclear migration; (3) the path of nuclear migration from cell to cell; and (4) the relation of nuclear migration to cytoplasmic streaming.<sup>1</sup>

#### II. MATERIAL AND METHODS

The experiments were made with Gelasinospora tetrasperma. This species, one of the Pyrenomycetes, was described by Dowding in 1933 (6). It resembles Neurospora tetrasperma in that its asci contain normally four bisexual spores and occasionally, in addition to bisexual spores, one or two dwarf unisexual spores. Some of these dwarf spores were isolated and sown on nutrient agar. In this way haploid mycelia were obtained.

Gelasinospora tetrasperma grows vigorously in culture and is devoid of secondary spores. The absence of secondary spores eliminates a possible source of contamination.

The fungus is known to include two races, a Canadian race and an English race, which are sexually incompatible with one another (6). Both these races were used, but most of the experiments were made with two haploid mycelia of the Canadian race. These mycelia will be referred to as mycelium no. 3 and mycelium no. 4. When mated they were found to be of opposite sex.

Difco malt-agar was used as a culture medium. To obtain the

<sup>&</sup>lt;sup>1</sup> An abstract of this paper was read at the Third International Congress for Microbiology, in New York, on September 7, 1939.

best experimental results it was found necessary to work with mycelia recently developed from spores and to place the cultures under favourable conditions of light and oxygen.

Age of mycelium. Unisexual mycelia that had been grown from dwarf spores and then stored in the refrigerator for five years were found to be unsuitable as material for the investigation because, when two of the mycelia of opposite sex were mated, they showed but limited nuclear migration.

For the critical experiments four unisexual mycelia obtained freshly from as many dwarf spores were employed.

Light. Both in darkness and in light rudiments of perithecia develop on bisexual mycelia in about three days; but the development of these rudiments into perithecia is strongly influenced by light.

Bisexual mycelia, when well illuminated, develop perithecia within five days; whereas, when kept in the dark, they produce perithecia only after the lapse of two weeks.

In the experiments here described, unless otherwise stated, the cultures were grown either in direct sunlight or about two feet from a 100-watt electric-light bulb which was kept running night and day. A shallow glass of water between the culture and the source of light prevented the agar from being dried by the heat of the lamp.

Oxygen. At first the Petri dishes and the test-tubes were sealed with strips of "parafilm" as a precaution against contamination; but this technique was abandoned when it was observed that perithecia do not develop in a vessel that is tightly sealed. Even without the parafilm, Petri-dish cultures grown in humid air may become sealed from within by an excessive growth of aerial mycelium, and then they do not fruit. On account of the adverse effect of sealing, the cultures were usually grown in Petri dishes without lids. The dishes were set on a glass plate and covered with a large glass vessel, and the vessel contained damp blotting paper placed in such a way as to reflect the light on to the cultures.

*Nuclei*. Material for studying the nuclei was fixed in Duggar's Gilson Fluid containing a few crystals of urea and then stained in 0.05 per cent Heidenhain's haematoxylin. The cytological work

was carried out while one of us (Dowding) was a guest of the Department of Botany at the University of Michigan.

#### III. DEMONSTRATION OF NUCLEAR MIGRATION

Convincing evidence that nuclei migrate from one mycelium into another was obtained as follows.

A large Petri dish, 15 cm. in diameter, was filled with agar. Mycelium no. 3 and mycelium no. 4, which were of opposite sex, were placed on opposite sides of the dish, and the agar in the centre was cut away so that the bottom of the dish became exposed

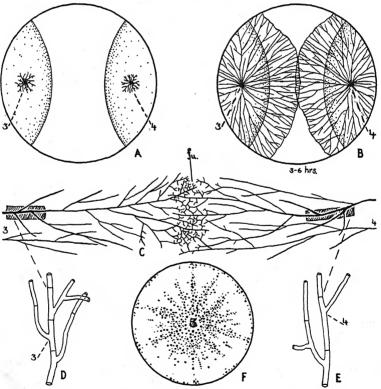


Fig. 1. Nuclear migration in Gelasinospora tetrasperma. Explanation in the text.

(FIG. 1, A). The two mycelia grew out past the agar and over the glass until they met (FIG. 1, B). They grew past each other

for a distance of about 2 mm., branched into a fine network, and fused with one another (FIG. 1, C). From three to six hours after fusion had been observed, a little sterile water was poured over the plate so that the hyphae would not adhere to the glass and then, with the aid of a binocular dissecting microscope, an area was chosen on the mycelium no. 3 side, about 5 mm. from the fusion zone, in which each hypha could be clearly seen to be part of mycelium no. 3. In this area a length of two or three cells of a main hypha was cut out and transferred to fresh agar (FIG. 1, C and D). The same procedure was carried out with a portion of the mycelium no. 4 (FIG. 1, C and E). In less than a week, the two cultures derived from the hyphal transplants of mycelium no. 3 and mycelium no. 4 had both produced perithecia. The perithecia on the transplant of mycelium no. 3 are shown in figure 1, F.

From the observations just described we may conclude that, in the mycelia shown in figure 1, C, nuclei had passed from mycelium no. 4 into mycelium no. 3 and from mycelium no. 3 into mycelium no. 4.

The experiment was repeated with this difference: that the time permitted to elapse after the two mycelia had fused and before hyphal transplants were made was lengthened to 24 hours in some plates and to 48 hours in other plates. It was then found that not one of the thirty-three transplants that were set on fresh agar produced perithecia. It would appear that within the 24 or 48 hours the migrating nuclei had migrated through and past the cells that had been transplanted.

#### IV. POSSIBILITY OF THE OVERGROWTH OF TWO MYCELIA

In Gelasinospora tetrasperma, when the mycelia nos. 3 and 4 are paired on an agar plate, the perithecia are frequently limited to the mycelium no. 4 (FIG. 4, A). In view of the results obtained in the experiment described in Section III, this distribution of perithecia is probably due to the migration of nuclei of mycelium no. 3 into mycelium no. 4. The alternative explanation is that the mycelium no. 3 overgrows mycelium no. 4, as suggested by Colson for Neurospora tetrasperma (3, p. 217). The experiment now to be described shows that, in Gelasinospora tetrasperma under cultural conditions, one mycelium does not overgrow another.

As material for the experiment both the Canadian race and the English race were employed. These races are sexually incompatible and, when paired, do not give rise to hybrid perithecia (6).

A Canadian unisexual mycelium and an English bisexual mycelium were paired on a plate. After seven days, the two mycelia had grown out, so that each occupied one-half of the plate, and perithecia had appeared on the bisexual mycelium (FIG. 2, A). A block of fresh agar was then placed on the top of the unisexual mycelium (FIG. 2, A); but, even after a month, no perithecia appeared on the block of agar or on any part of the half of the dish occupied by the unisexual mycelium (FIG. 2, A).

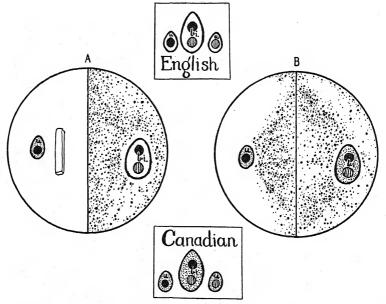


Fig. 2. Gelasinospora tetrasperma. One mycelium does not overgrow another. Explanation in the text.

It thus appears that, in the experiment, the bisexual mycelium remained limited to that half of the dish in which it was planted and did not overgrow or intermingle with the unisexual mycelium.

A Canadian unisexual mycelium and a Canadian bisexual mycelium were paired on a plate. In this experiment, unlike the one just described, perithecia appeared on both sides of the plate (FIG.

2, B). Here the two mycelia, both belonging to the Canadian race, were sexually compatible, and nuclei of the required sex migrated from the bisexual into the unisexual mycelium.

The two experiments just described and illustrated in figure 2 were repeated several times and always with the same result.

#### V. SPEED OF NUCLEAR MIGRATION

To measure the speed of nuclear migration and to compare it with the hyphal growth-rate, two sets of experiments, A and B, were made. An account of these experiments will now be given.

A. Paired mycelia. Inocula of the two unisexual mycelia, nos. 3 and 4, were placed on opposite sides of an agar plate and were allowed to grow until they met (Fig. 3, A). A millimeter scale was then drawn with ink on the bottom of the plate in such a way that the zero mark was on the meeting line of the two mycelia (Fig. 3, A).

Five hours after the two mycelia had met, six transfers were made from the plate to tubes of fresh agar. Three of the transfers were taken from mycelium no. 3 and three from mycelium no. 4; and, on each side of the median meeting line, they were taken at distances of 15 mm., 20 mm., and 25 mm. (FIG. 3, A). Within a week two of the six transfers had produced perithecia, while the other four remained sterile. The transplants for the two tube cultures that fruited were taken as follows: one 15 mm. and the other 20 mm. from the meeting line on the mycelium no. 4 side of the dish.

On repeating the experiment just described, once more two of the six transfers fruited and again one of the transfers had been taken 15 mm. and the other 20 mm. from the meeting line of the two mycelia. However, in this experiment, the mycelium that yielded the fruiting transfers was mycelium no. 3 and not mycelium no. 4.

We may conclude: (1) that, in the first of the two experiments just described the nuclei of mycelium no. 3 travelled into mycelium no. 4; (2) that, in the second experiment, the nuclei of mycelium no. 4 travelled into the mycelium no. 3; (3) that, in both experiments, the migrating nuclei travelled a distance of 20 to 25 mm.

in five hours; and (4) that the velocity of the migrating nuclei was 4 to 5 mm. per hour.

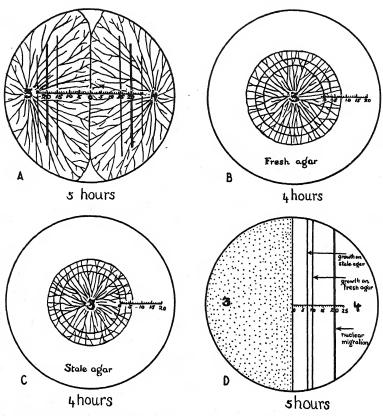


Fig. 3. Gelasinospora tetrasperma. Speed of nuclear migration, and a comparison of this speed with the growth-rate of the hyphae. Explanation in the text.

Two more plates were inoculated with mycelium no. 3. One contained fresh malt-agar (FIG. 3, B) and the other staled maltagar (FIG. 3, C). The staled agar was obtained by melting the agar of a two-day-old culture of mycelium no. 4 by heating it over warm water and then pouring the melted agar on to a fresh plate and discarding the mycelium. After the inoculum of mycelium no. 3 had grown out a short distance into the agar in the two plates, the increment of growth was recorded every two hours by

ringing the edge of the mycelium on the under side of the dish with ink (FIG. 3, B and C). The radial growth rate of mycelium no. 3 was found to be: on fresh agar, 2 mm. per hour; and on agar staled by mycelium no. 4, 1.5 mm. per hour.

Figure 3, D, shows diagrammatically the results of the experiments illustrated in figure 3, A, B, and C. In a period of five hours, mycelium no. 3 grew on fresh agar 10 mm. and on stale agar 7 mm. and the nuclei of mycelium no. 3 migrated into the mycelium no. 4 a distance of at least 20 mm. From these data we may conclude that the rate of movement of the nuclei was twice the rate of hyphal growth on fresh agar and nearly three times the rate at which the hyphae would have grown had one mycelium overgrown the other and thus had been forced to make its way through stale agar.

B. Patched mycelia. Two mycelia of Gelasinospora tetrasperma of opposite sex were grown for two days on two agar plates. One of the two mycelia was then used to patch the other: from one dish a small rectangular piece of hyphae-containing agar (10  $\times$  5 mm.) was cut out, and it was set upside down on the mycelium in the other dish along a radius of the dish and about half way between the centre of the dish and the periphery. In about a week, perithecia formed on the agar surrounding the patch and as far away from the patch as 15 mm. (Fig. 4, D). Patched mycelia were employed in a second method devised for measuring the speed of nuclear migration. An experiment made with patched mycelia will now be described.

Three patches of mycelium no. 3 were applied to a plate containing mycelium no. 4. Ten hours later, three transfers were removed from the agar surrounding each patch at distances of 5 mm., 10 mm., and 15 mm. from the edge of the patch. The transfers removed at distances of 5 mm. and 10 mm. from the patches produced perithecia, but those removed at a distance of 15 mm. remained sterile.

In the experiment just described the nuclei derived from the patch of mycelium no. 3 must have travelled through the hyphae of mycelium no. 4 a distance of 10 mm. in 10 hours, or at a speed of one mm. per hour. This speed is much less than the speed of from 4 to 5 mm. per hour obtained in the experiments made with

paired mycelia. The relatively low speed of nuclear migration in the patched mycelium may well have been due to the fact that, in cutting out the patches, the hyphae along the edges of each patch were severed by the knife and thus injured. However, a speed of one mm. per hour exceeds the rate of elongation of the hyphae, as will now be shown.

Two patches of mycelium no. 3 were applied to two agar plates of which one contained fresh malt-agar and the other stale agar obtained from a culture in which mycelium no. 4 had been growing for two days. Ten hours after the plates had been inoculated, the hyphae in the patch on the fresh agar had grown out 7 mm. while the hyphae in the patch on the stale agar had grown out 6 mm. It is obvious that these growth rates, 0.7 mm. per hour and 0.6 mm. per hour respectively, are much less than the rate of nuclear migration, namely, 1.0 mm. per hour, obtained in the preceding experiment.

### VI. THE EFFECT OF LIGHT ON NUCLEAR MIGRATION

As has already been remarked, when mycelia nos. 3 and 4 are paired, the perithecia frequently are limited in their distribution to mycelium no. 4 (FIG. 4, A). Sometimes, however, the reverse is true and the perithecia are limited to mycelium no. 3.

To find some reason for the variation in the distribution of perithecia just described, experiments were devised in which each plate of paired mycelia was unevenly illuminated and then the resulting distribution of perithecia was observed.

A. Half of each culture illuminated. Half of the lid and half of the container of each of twenty pairs of Petri dishes were painted black outside. The lids and containers were put together so that one side of each culture would be almost completely in the dark. The twenty dishes were each inoculated on opposite sides with mycelia nos. 3 and 4 in such a way that there were ten dishes with mycelium no. 3 in the blackened half and ten dishes with mycelium no. 4 in the blackened half. The cultures were grown under an electric-light bulb for six days and then examined. The distribution of the perithecia was as follows.

Of the twenty cultures, thirteen had perithecia on the lighted mycelium only; three had most of the perithecia on the lighted

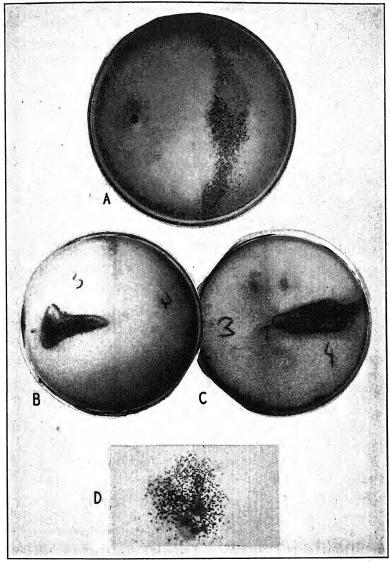


Fig. 4. Gelasinospora tetrasperma. Nuclear migration. A: mycelia nos. 3 and 4 mated; perithecia have formed on mycelium no. 3. B and C: effect of light on nuclear migration; in B part of mycelium no. 3 was illuminated and in C part of mycelium no. 4; perithecia have been formed in the illuminated parts of the mycelia. D: mycelium no. 3 patched with mycelium no. 4; perithecia have been formed on the agar surrounding and at some distance away from the patch of mycelium no. 4. Magnification: A, B, and C, about half the natural size; D, slightly less than natural size.

mycelium; three had perithecia equally on the lighted and darkened mycelia; and one was sterile.

It is evident that, in the experiment just described, the perithecia occurred most frequently on the illuminated mycelium, thus showing that light favoured their development. The darkened mycelium, whether no. 3 or no. 4, seldom produced any perithecia.

After the distribution of the perithecia in the experiment just described had been noted, transfers were taken from a darkened and sterile mycelium no. 3 and from a darkened and sterile mycelium no. 4, whose lighted mates had produced perithecia, and these transfers were grown separately in the light for two weeks. They failed to produce any perithecia and thus revealed that they had remained unisexual. Nuclei of opposite sex could not have migrated into them.

B. A small area of each culture illuminated. Four Petri dishes were each inoculated on opposite sides with mycelia nos. 3 and 4. They were then wrapped in black paper in which a small hole had been cut through which light could pass. The holes were arranged so as to be: in two of the plates over mycelium no. 3, and in the two other plates over mycelium no. 4. The plates were then placed under an electric-light bulb. At the end of a week perithecia had begun to be formed. Four days later the lids of the Petri dishes were removed and the cultures were examined. It was found that the perithecia were distributed chiefly in that part of the plate that had been illuminated regardless of whether the illuminated mycelium had been no. 3 or no. 4 (FIG. 4, B and C).

From the results of the experiments described above under A and B we may conclude that, in *Gelasinospora tetrasperma*, during the initiation of the sexual process, light influences the migration of nuclei of one sex into the mycelium of opposite sex in such a way that the nuclei tend to pass out of a darkened mycelium of one sex into the illuminated part or parts of the mycelium of opposite sex.

The direction of nuclear migration is influenced not only by light but by other conditions. This was made clear when mycelia nos. 1 and 3, which were of opposite sex, were patched in both the possible ways and under identical conditions of illumination. It was found that: when patches of mycelium no. 1 were placed on

cultures of mycelium no. 3, mycelium no. 3 soon produced perithecia around the patches; but that, when patches of mycelium no. 3 were placed on cultures of mycelium no. 1, in none of about a dozen experiments did any perithecia appear around the patches on mycelium no. 1.

#### VII. THE PATH OF NUCLEAR MIGRATION

Two plates were inoculated, one with mycelium no. 3 and the other with mycelium no. 4. Then the plates were bridged by means of a strip of cover-glass 2 mm. wide in the manner shown

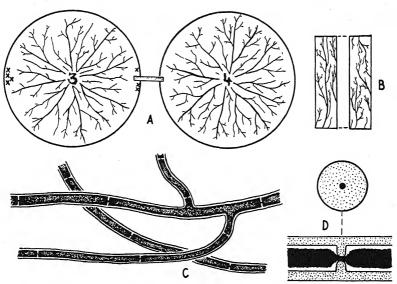


Fig. 5. Gelasinospora tetrasperma. The path taken by migrating nuclei. Explanation in the text.

in figure 5, A. At the end of six days the two mycelia had covered the agar and about twelve hyphae had grown on to the bridge (FIG. 5, A and B). The bridge was then removed and the plates were separated. Six days later perithecia appeared in the dish containing mycelium no. 3 in the positions shown in figure 5, A by means of crosses.

In the meanwhile, the cover-slip bridge (FIG. 5, B) was mounted on a slide and the hyphae upon it were treated first with iodine in potassium iodide to stain the protoplasm deep-brown and after-

wards with chlor-zinc iodine to swell the cell-walls (2, pp. 89-91). It was then found that, as already described by Buller for the mycelia of Pyrenomycetes and Discomycetes in general (2), every hypha on both surfaces of the bridge had a protoplasmic strand passing from one cell to the next through the central pore of each septum (FIG. 5, C and D). It was also observed in studies of the living hyphae of Gelasinospora tetrasperma that each new septum is formed near the end of an elongating hypha as an annular ingrowth from the lateral wall and that it completes its development, with reduction of the open pore to the minimum width, in about thirty minutes. It must therefore be admitted that, in the experiment illustrated in figure 5, A, nuclei which passed from mycelium no. 4 across the cover-glass bridge into mycelium no. 3 must have passed through the septal pores actually shown, or like those shown in figure 5, C and D. This is the first time that experimental evidence has been obtained that proves conclusively that migrating nuclei in an Ascomycete are able to pass via septal pores from one cell to the next.

## VIII. NUCLEAR MIGRATION AND CYTOPLASMIC STREAMING

It has been shown by Buller (2) that, in the Pyrenomycetes, Discomycetes, and Hymenomycetes, as a hypha elongates, cytoplasm is constantly flowing toward the growing point. Thus the growth of a hypha is in part due to the extension of the cell-wall at the tip of the hypha and in part due to the newly created space in the terminal cell of the hypha being constantly filled up by cytoplasm that flows to the tip of the hypha from the column of cytoplasm in the terminal and subterminal cells.

In Gelasinospora tetrasperma, with the low power of the microscope, it can readily be seen that the column of cytoplasm in the terminal and subterminal cells of a growing hypha is continuously flowing toward the growing point, and it was found that this flow can be beautifully demonstrated by means of a moving-picture film.

In Gelasinospora tetrasperma the column of cytoplasm that flows toward the tip of each growing hypha passes from one cell to the next by way of the central perforation in each septum, *i.e.* in the

same manner as that observed by Buller (2) in Pyrenomycetes, Discomycetes, and Hymenomycetes in general.

In Gelasinospora tetrasperma, in a subterminal cell exhibiting streaming, one gains the impression that all the protoplasmic contents are streaming with the exception of a vacuole which is frequently pressed against the distal septum. This question therefore arises: are or are not the nuclei carried in the column of streaming cytoplasm from one cell to the next as it flows toward the hyphal tip? If the nuclei are carried in this way, the younger cells near the hyphal tips should contain more nuclei than the older highly vacuolated cells of the mycelium from which the massive part of the cytoplasm has already flowed. To compare the number of nuclei in young and old cells of hyphae exhibiting streaming, we proceeded as follows.

Two Petri dishes, A and B, each containing a glass slide, were filled with agar so that the slides were just immersed, and they were then inoculated with a mycelium of *Gelasinospora tetrasperma*. In dish A the inoculum was placed some distance away

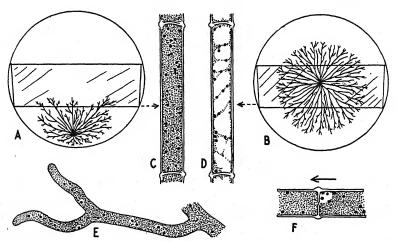


Fig. 6. Gelasinospora tetrasperma. The nuclei in the cells remain fixed while cytoplasm flows toward the tips of the growing hyphae. Explanation in the text. Magnification: C-F, 575.

from the slide, while in dish B the inoculum was placed upon the middle of the slide (Fig. 6, A and B). After about twelve hours the plates were examined. In dish A the mycelium had reached

the slide and four hyphae had grown on to it for a distance of about 1 cm. Every main hypha exhibited cytoplasmic streaming toward the hyphal tip. All of these hyphae were completely filled with protoplasm or contained a few small vacuoles. In dish B the mycelium had covered the slide and grown out over the agar beyond it for a distance of several centimeters. The main hyphae on the slide showed rapid cytoplasmic streaming toward the hyphal tips. All the older parts of the hyphae were highly vacuolated and showed only a few cytoplasmic strands remaining in each cell.

The two slides (Fig. 6, A and B) were fixed and stained to show the nuclei and then cut away from the rest of the agar in the dishes. The preparations were then mounted in glycerine.

For comparison, two typical cells approximately equal in length and in diameter were chosen, one on the slide of culture A (FIG. 6, A) and the other on the slide of culture B (FIG. 6, B); and then their nuclei were counted. In the comparatively empty cell of culture B (FIG. 6, D) there were 25 nuclei, while in the densely filled cell of culture A there were 22 nuclei (FIG. 6, C). Also observations made on many other cells on the slides of cultures A and B showed that, although the number of nuclei in a cell was distinctly variable, in general there were no fewer nuclei in old empty cells than there were in young densely filled ones.

The hyphal tips were also examined and they were found to contain nuclei which were at about the same distance from one another as were the nuclei in the vacuolated cells (Fig. 6, E).

A characteristic type of young cell on the slide of culture A was one densely filled with protoplasm with the exception of a vacuole occupying about half the diameter of the hypha and pressed against the septum (Fig. 6, F). Such a cell was found to contain about twenty nuclei, and four or five of these could be seen in the extremely thin lining layer of cytoplasm surrounding the vacuole where, from our experience of living material, there is no streaming (Fig. 6, F).

From the foregoing observations we may conclude that, when cytoplasm is being evacuated from older cells in a mycelium and is passing to the hyphal tips, the nuclei of the older cells are not carried away in the cytoplasmic stream, but remain anchored to the cytoplasm which forms a very thin layer that is pressed close

against the cell-walls and forms the bounding layer of the vacuoles.

That, in a cell through which cytoplasm is rapidly streaming, the walls of the vacuoles are fixed and do not flow with the stream was discovered by Buller (1, p. 129) who observed that, in *Pyronema confluens*, tiny solid bodies (his *Woronin bodies*) embedded in the walls of the vacuoles remain at rest while the cytoplasmic stream flows past them.

The mechanism which enables nuclei to migrate from a mycelium of one sex into that of another sex in such a fungus as *Gelasinospora tetrasperma* is at present unknown. There is at present no reason to suppose that the migration is dependent on the mass movement of cytoplasm which normally takes place in all growing hyphae and is always toward the growing points.

In Gelasinospora tetrasperma, nuclei of mycelium no. 4 must have moved clear across the mycelium no. 3 shown in figure 5, A; for, otherwise, perithecia could not have formed in the positions shown by the crosses; and in the Hymenomycete, Coprinus lagopus, Buller found that nuclei of one sex can migrate many centimeters across the middle of a large haploid mycelium of opposite sex (1, p. 233). To discover what causes nuclear movement during the migration of nuclei under conditions such as those just described is one of the tasks of the future.

#### SUMMARY

- 1. In *Gelasinospora tetrasperma*, one of the Pyrenomycetes, the migration of nuclei from a mycelium of one sex into a mycelium of opposite sex has been confirmed.
- 2. Migrating nuclei have been found to travel through a mycelium at a speed of from 4 mm. to 5 mm. per hour.
- 3. It was shown that two mycelia of opposite sex, on coming into contact on an agar plate, fuse with one another but do not overgrow one another and that the speed of nuclear migration may be twice or three times the rate at which living hyphae grow in length.
- 4. Light influences the migration of nuclei. In mating experiments it was found that nuclei move from a darkened mycelium of one sex toward and into an illuminated part of a mycelium of opposite sex.

- 5. Migrating nuclei move from cell to cell via the minute central pore in the transverse septum.
- 6. In Gelasinospora tetrasperma, as in other Pyrenomycetes, columns of cytoplasm are constantly flowing toward the tips of the growing hyphae. When cytoplasm is being evacuated from older cells in a mycelium and is passing toward the growing hyphal tips, the nuclei of the older cells are not carried away in the stream of cytoplasm but remain anchored to the thin fixed layer of cytoplasm that is pressed against the cell-wall and that forms the bounding layer of the vacuoles.
- 7. The mechanism which enables nuclei to migrate from a mycelium of one sex into and along a mycelium of opposite sex is at present unknown.

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# NOTES ON GYMNOSPORANGIUM CUPRESSI

W. H. LONG AND L. N. GOODDING

(WITH 1 FIGURE)

This paper describes the pycnial and aecial stages of *Gymnosporangium Cupressi* on *Amelanchier mormonica* (?), gives an emended description of the telial stage and new data on hosts and distribution.

The telial stage of this rust was discovered by Goodding at Snebly Hill near Sedona, Arizona, in 1919 and described in 1921. Every year since finding this rust both authors have searched for the aecial stage but without success until the year 1939.

In January 1937, Ranger David J. Stouffer of the Forest Service found the telial stage of this Gymnosporangium at Webster Springs (formerly Sawmill Springs) which is about 20 miles north of Clifton, Arizona. The galls of the rust were very common over this area, much more so than in the type locality near Sedona, for this reason the Webster Springs area was chosen during the past few seasons for intensive search for the aecial stage. Another reason for favoring this locality was the fact that junipers are not abundant in this area. No junipers occur within a half a mile radius of the place where the aecia were finally located. The authors realize that rusts do not respect such boundaries and that this aecial infection might be due to a Gymnosporangium on a juniper. The probability, however, of its being caused by G. Cupressi is much greater. Below Webster Springs, a line of heavy infection on Cupressus occurs along the sides of a deep draw or ravine. A second line of heavy infection follows a side draw. These two lines of infection seem to follow natural air channels which converge at a point in the main ravine where the infected Amelanchier was found. Adjacent to the Amelanchier bushes is a 15-foot Cupressus tree plastered with galls on twigs and small branches. So heavy was this infection that many of the twigs

<sup>&</sup>lt;sup>1</sup> Long, W. H. Notes on new or rare species of rusts. Bot. Gaz. 72: 39-44. 1921.

were killed. It, therefore, seems reasonable to assume that the aecia discovered on the *Amelanchier* leaves are those of *G. Cupressi*; furthermore the characteristics of these aecia do not correspond to any known species of *Gymnosporangium*.

The type description of this rust gives Cupressus arizonica Greene as its host; later investigations show that the host is C. arizonica var. bonita Lemm. (C. glabra Sudw.) since this is the only species growing in the Sedona area (type locality). The Cupressus at Webster Springs is the true C. arizonica, in fact this general area is the type locality for this species. This makes two hosts for the telial stage of this rust—C. arizonica and C. arizonica var. bonita; also two widely separated localities—the Sedona area in Coconino County and the Webster Springs area in Greenlee County (formerly a part of Graham County). This Gymnosporangium probably occurs on these two hosts throughout their range where associated with species of Amelanchier.

### Gymnosporangium Cupressi

O. Pycniis epiphyllis, minutis, 150-200 microns latis.

- I. Aeciis hypophyllis, cylindraceis, 3–5 mm. altis, 0.2–0.3 mm. latis, ad apicem non vel vix ruptis, tandem ad latera longitudinaliter fissis; aeciosporis globosis vel angularis, 16.8–18.6 × 21–24.8 microns, episporio 3–4 microns crasso, poris germantionis 5, sparsis.
- O. Pycnia epiphyllous, gregarious, on pallid spots, rather conspicuous, becoming blackish-brown, globoid, 150–200 microns in diameter.
- I. Aecia hypophyllous on thickened discolored spots, few, solitary or in small groups, cylindrical, 3–5 mm. high by 0.2–0.3 mm. in diameter; peridium white (hyaline), tardily if at all dehiscent at apex, slowly rupturing by longitudinal slits along the sides; peridial cells usually seen in face view, not hygroscopic, remaining straight when wet, linear-oblong to oblong-lozenge-shaped in face view,  $16-18 \times 62-93$  microns, linear-oblong to oblong in side view 20-27 microns thick, the outer wall thin, 1-1.5 microns, smooth, the inner and side walls 5–7 microns thick, closely verrucose-rugose with irregular ridge-like papillae; aeciospores angular to globoid,  $16.8-18.6 \times 21-24.8$  microns; walls chestnut-brown, 3–4 microns thick, very minutely and closely verrucose-rugose, appearing almost smooth, germ pores large, evident, 5, scattered.

On Malaceae. Collected on Amelanchier mormonica (?) C.

Schneid., Webster Springs, 20 miles north of Clifton, Arizona, on Coronado Trail, October 6, 1939, by Leslie N. Goodding and T. D. Mallery (No. 8439 Long) at 7,000 ft. elevation.

III. Telia caulicolous, from a perennial mycelium, appearing on twigs, branches and trunks, causing fusiform to subglobose galls

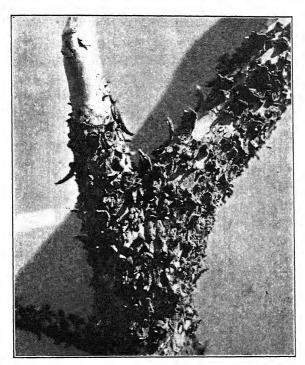


Fig. 1. Gymnosporangium Cupressi.

with bark much roughened and exfoliating (FIG. 1), 0.4–90 cm. long by 0.5–30 cm. thick, usually breaking forth irregularly and often transversely on the smaller branches and twigs, in irregular rows in deep longitudinal fissures of the bark on the larger branches and trunks, emerging in oval to elliptical sori,  $0.5–2 \times 1–5$  mm., at first partially covered by the rupturing bark, later this bark may fall away entirely leaving the sori naked, or the bark may persist as an irregular cup around the sori, telia at this stage flat, firm, chestnut-brown, when mature, more or less tongue-shaped, often irregular and somewhat crenate at top, before gelatinizing 2–10 mm. broad by 4–6 mm. tall, dark chestnut-brown, becoming cinnamon-brown after expansion; teliospores 2-celled, spores with col-

ored walls oval to ellipsoid, 20– $27 \times 30$ –50 microns, slightly or not at all constricted at septum, the two cells subequal; walls 2–3 microns thick, fulvous, germ pores two in each cell near septum; pedicel solid, hyaline, cylindrical, 3–4 microns thick, 100–175 microns long; teliospores with thin, colorless walls, oblong to narrowly ellipsoid, not constricted at septum, 16– $20 \times 40$ –60 microns, the two cells subequal, spores rounded at both ends, germ pores two in each cell at septum, walls 1–1.5 microns thick.

On Juniperaceae. Type collected on *Cupressus arizonica* var. bonita Lemm. (C. glabra Sudw.) at Snebly Hill near Sedona, Ariz., May 26, 1920, by *Leslie N. Goodding* (No. 6906 Long); also same host and locality in 1919 (No. 6903 Long); on same host on Cottonwood-Sedona road, 6 miles from Sedona, May 26, 1920 (No. 6904 Long).

On Cupressus arizonica Greene near Webster Springs about 20 miles north of Clifton, Ariz., January 12 and March 13, 1937, by David J. Stouffer (Nos. 8052 & 8092 Long); on same host and same locality, May 7, 1937, by Leslie N. Goodding (No. 8192 Long).

## DEVELOPMENT OF THE CARPOPHORES OF CERTAIN BOLETACEAE

R. P. ELROD 1 AND WALTER H. SNELL

(WITH 2 FIGURES)

The available information concerning the development of the carpophore of the Boletaceae is very incomplete. At present it consists of a few fragmentary statements, some speculative conclusions and only a few well worked-out studies. It is desirable that the facts be obtained because in the past some taxonomic arrangements of the higher fungi have been based fundamentally upon the type of development of the carpophore and because such distinctions may be of contributory, if not fundamental, importance in the classification of the Boletaceae. This paper adds studies of three species of *Boletus* in the group Viscipelles of Fries and Peck (genus *Ixocomus* Quélet of the Europeans) and two species of *Boletinus*.

DeBary (1, pp. 287–290) stated that *B. luteus* L. ex Fries, *B. elegans* Fries and their relatives are angiocarpic because of marginal veils, while other species are gymnocarpic. J. Schroeter (8, p. 62) placed the Boletaceae in his Hemiangiocarpeae. P. Hennings (4, p. 108) stated that certain of the species of this family have their tubes exposed from the beginning (hence, are gymnocarpic). Patouillard (7, p. 34) divided his "Basidiomycètes homobasidiés normaux" into gymnocarpic "Aphyllophoracés," hemiangiocarpic "Agaricés" (in which the Boleti and Paxilli were included as the Boletés), and the angiocarpic Gasteromycetes, fundamentally on the basis of the characters as stated.

In a complete study of *B. Zelleri* Murr., Zeller (10) showed that the first development is a cleavage plane from the outside inward, which forms an annular furrow. A palisade then de-

<sup>&</sup>lt;sup>1</sup> A large portion of the material presented in this paper formed a part of the thesis presented by the first author in partial fulfillment of the requirements for the degree of Master of Science in the Department of Botany in the Graduate School of Brown University, May, 1938.

velops on both the upper and lower surfaces of this furrow. Hence, this species is gymnocarpic.

Yates (9, pp. 229 and 234) made the statement that his incompleted study of *B. granulatus* L. ex Fries confirms the conclusions of Zeller with *B. Zelleri*. He adds that he has found a definite veil in young plants of *B. edulis* Bull. ex Fries and *B. chrysenteron* Bull. ex Fries 10–15 mm. high, but in both cases the veil entirely disappears, leaving no trace either of annulus on the stipe or of fringe on the margin of the pileus. No details were given by Yates for either of these situations. One is left to conclude that he referred, not to a universal veil in any sense, but to a marginal veil formed by the outgrowth of the incurving margin of the pileus, which reaches and makes contact with the stipe, as found in other species by Kühner and by the authors of this paper.

Kühner (5) found that B. parasiticus Bull. ex Fries is gymnocarpic, with a development very similar to that of B. Zelleri. On the other hand, in the annulate B. flavus With. ex Fries (B. elegans Fries?), in the very youngest stages, as the pileus enlarges and as the stipe is forming a true hymenium with basidia and cystidia, the margin tends to incurve. As further enlargement takes place, the margin soon makes contact with the hymenial surface of the stipe, producing inside this false veil a cavity in which the hymenium shortly is formed. He called this type of development pseudoangiocarpic, rather than hemiangiocarpic. Kühner also states that B. viscidus and probably all annulate species of Ixocomus are similarly pseudoangiocarpic. In a later paper (6), he stated that Gyrodon lividus (Fries ex Bull.) Sacc. is gymnocarpic and he showed that Boletinus cavipes (Opat.) Kalchbr. is pseudoangiocarpic like Boletus flavus, with a development similar to it except that in the former only the upper portion of the stipe is fertile instead of the entire length as in B. flavus.

Gilbert (3), in his characterizations of the genera of his order Boletales, included the following descriptive terms: Boletinus at first gymnocarpic, then pseudoangiocarpic; Ixocomus—gymnocarpic, sometimes pseudoangiocarpic; Boletellus and Strobilomyces—probably gymnocarpic, then pseudoangiocarpic; Paxillus, Phylloporus, Xerocomus, Boletus, Krombholzia, Porphyrellus, Gyroporus, Gyrodon and Boletinellus—all gymnocarpic.

#### BOLETUS PLACIDUS BON.

In the smallest specimens of this species examined, 250–300  $\mu$  broad and 2.8 mm. tall (FIG. 1, A), a pileus of irregular shape is already present, often somewhat broader than the stipe portion and with a slight constriction at the apex of the stipe. The tissue of this primordium of the pileus is undifferentiated, but there are loose projecting hyphae on the margin. The stipe already has a palisade on its surface and glandular dots of caulocystidia.

In the  $500 \,\mu$  stage (Fig. 1, B), there is considerable constriction of the apex of the stipe, and the pileus, although still irregular in shape, has become more like the normal form of mature specimens. The upper portion of the pileus flesh has become somewhat looser than the remainder and there is a beginning of a dermal layer of overlapping hyphae. On the lower side of the pileus, ends of hyphae have bent down perpendicular to the surface to form a palisade. No change can be noted in the stipe tissue.

In the 650–700  $\mu$  stage, 2.5 mm. tall (FIG. 1, C), there is no constriction of the apex of the stipe. The pileus is still irregular in outline, with a margin very much incurved toward the stipe, and the marginal hyphae, appearing like a brush in the sections, extend nearly to the surface of the stipe. The surface layer of the pileus has become slightly compacted. On the stipe, the only change is that the clusters of the cystidia have become more abundant.

In the stage 1.36 mm. broad and 3 mm. tall (FIG. 1, D), the pileus has become regular in shape, and the margin is still incurved, but the marginal hyphae have not yet reached the stipe. There has been no change in the flesh, but there is a surface layer of more or less erect, slightly tangled hyphae 110–145  $\mu$  long, 3–3.5  $\mu$  thick, which does not extend quite to the extreme margin. The hymenium is now compact and fairly well formed. It has no mature basidia, but has a few isolated cystidia and a few glandular dots of cystidia near the stipe. The stipe itself is thickly glandular-dotted two-thirds to the base and the lower portion of its flesh has become looser in the center.

In the 1.6 mm. stage, 5 mm. tall (FIG. 1, E), the marginal hyphae have made contact with the stipe in a compact mass, but have not

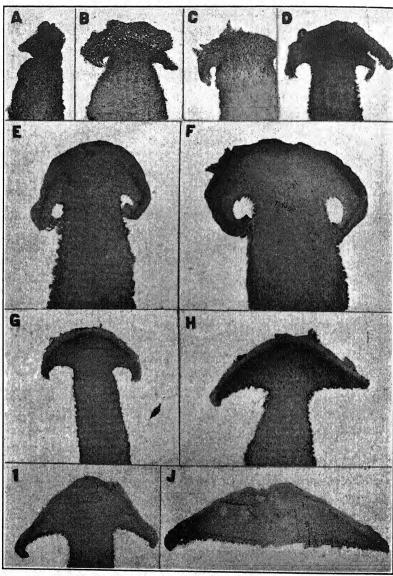


Fig. 1. Development of the carpophore of Boletus placidus. A, first stage of pileus evident,  $250-300\,\mu$  broad, and stipe with a palisade on the surface and glandular dots and caulocystidia,  $\times$  50. B,  $500\,\mu$  stage, showing evidence of a dermal layer, with incurved, hairy margin and palisade of parallel hyphae on lower side of pileus,  $\times$  50. C,  $650-700\,\mu$  stage showing little advance except the increasing prominence of the glandular dots of the stipe,  $\times$  50. D, about 1.4 mm. broad, with primordial ixotrichoderm on

at all become fused with it. The surface layer of more or less erect hyphae now extends entirely to the beginning of the outgrowth of marginal hyphae and is 160 µ thick on top, but thinner toward the margin. The hyphae are now less distinct because they have become partially gelified. For a covering of this type, which ultimately makes a viscid, viscous or glutinous surface in many Boletaceae and which is probably of the same sort in agarics, if not in other groups, the second author has been using the term "ixotrichoderm" (2, p. 699, footnote 2). Beneath this layer of gelifying hyphae, extending from the margin inward nearly to the flat dome of the top of the pileus there is a narrow. darker-appearing zone of compacted hyphae which has the appearance of a cutis, but which from its position probably should be termed a subcutis. The hymenial palisade now extends half way to the margin, and has more cystidia, and a few matured basidia bearing spores. There is no change in the condition of the stipe.

In the next stage, with the pileus about 2.5 mm. broad and 5.5 mm. tall (Fig. 1, F), the only noticeable changes are as follows:—the tissue of both pileus and stipe is more loosely tangled; the hymenium has glandular dots all over its surface; and the stipe is glandular-dotted to the base.

In the next stage, about 3 mm. broad and 7 mm. tall (Fig. 1, G), the pileus is partially expanded. The margin has pulled away from the stipe, is now somewhat curved but practically vertical, and there are no signs of the marginal hairs on the stipe to form any semblance of an annulus. The ixotrichoderm has a somewhat different appearance. In the layer of gluten are hyphae that appear fresh and new because of their sharpness of outline, regularity and deep-staining quality. The suggestion is that the first hyphae of the layer became completely gelified and that new ones have grown up from the compacted layer (which now completely covers

surface, well-developed hymenium and prominent glandular dots on the stipe,  $\times$  25. E, 1.6 mm. broad, with ixotrichoderm partly gelified and marginal hyphae in contact with the stipe forming a chamber around the developing hymenium,  $\times$  25. F, 2.5 mm. stage showing marginal hyphae appressed to stipe but not fused with it,  $\times$  17. G, about 3 mm. broad, with margin pulled away from the stipe and no sign of marginal hairs or of annulus,  $\times$  12. H, 3.5-4 mm. broad, with pileus farther expanded and hymenophore somewhat undulated,  $\times$  12. I, about 5.4 mm. broad,  $\times$  8. I, pileus 8 mm. broad,  $\times$  8.

the pileus) to continue the production of gluten. The hymenium is seemingly more compact and more chromophilous, with abundant glandular dots, but still with few mature basidia. The stipe has changed only to the extent that the flesh has become longitudinally areolate and looser toward the base.

In the stage 3.5–4 mm, broad and 11 mm, tall (Fig. 1, H), the pileus has become expanded into its mature shape, although the margin is somewhat curved, and wadded or tufted. The condition of the ixotrichoderm is about the same, in that no further gelification is evident. The hymenophore has begun to undulate, the folds covered with palisade are about 50  $\mu$  high, and the glandular dots are prominent. In the stage about 5.4 mm, broad (Fig. 1, I), the only change is the somewhat greater height of the hymenial folds (65  $\mu$ ), but in the 8 mm, stage (Fig. 1, I), the pileus has become expanded, any marginal hyphal wad has disappeared and the tube-wall primordia are 1.5 mm, long.

Boletus placidus is therefore pseudoangiocarpic in development like B. flavus and Boletinus cavipes, in that the hymenophore begins its development in the open, later becomes enclosed in a cavity by the incurving of the margin of the pileus and the development of the marginal hyphae which make contact with the stipe, and then completes its development in the open as the margin pulls away from the stipe. As far as is known to the authors, this is the first reported case of pseudoangiocarpy in exannulate forms of the Boletaceae.

#### BOLETUS GRANULATUS AND B. AMERICANUS

The development of B. granulatus (FIG. 2, A–E) and B. americanus (FIG. 2, F–H) is in each case approximately the same as that of B. placidus. They both start when 250–400  $\mu$  broad to enlarge slightly at the tip of the stipe, and at about 400–500  $\mu$  the margins of both begin to curve toward the stipe, finally reach it and then separate without leaving any semblance of annular material on the stipe. Also, the development of the viscous layer on the pileus, of the glandular dots on the stipe, and of the hymenium is about the same in all three species.

In B. granulatus, however, the contact of the marginal hairs with the stipe occurs somewhat earlier than in B. placidus, when

the young pileus is 700–800  $\mu$  broad, and the margin breaks away somewhat earlier, at about the 2.3 to 2.4 mm. stage. Further, in B. granulatus, the hymenial palisade does not appear at the apex of the stipe until the pileus has reached about 500  $\mu$  in breadth, whereas in the other two species it appears in the 300–400  $\mu$  stages. Likewise, the first spores are not produced until a little later than in the other two species—i.e., at about the 2 mm. stage instead of the 1.6 to 1.9 mm. stages in the others.

Boletus americanus differs from the other two species in only two minor respects. For one thing, in the material available, the making of contact of margin with stipe was found to be irregular. In some series of specimens, this contact has been made in stages as small as 1.15 mm. broad and in others, not until stages as large as 2.3 mm. Then again, the surface clothing in some of the younger specimens is more of an ixocutis than an ixotrichoderm—that is, the projecting surface hyphae which would later gelify to form the viscous layer are often flat and parallel to the surface rather than wavy-erect.

Both *B. granulatus* and *B. americanus* are therefore pseudo-angiocarpic in development, like *B. placidus*. This was to be expected in this subgroup of closely related species with glandular-dotted stipe in the Viscipelles (or new genus *Ixocomus*). Yates' implication (*loc. cit.*) that the development of *B. granulatus* is gymnocarpic, with the hymenium forming externally in an annular groove or furrow as in *B. Zelleri*, was apparently based upon a study of insufficient material.

# SUMMARY OF THE VISCIPELLES OF THE GENUS BOLETUS (GENUS IXOCOMUS QUÉLET)

Thus far, the development of four species of the Viscipelles has been studied completely—the annulate B. flavus (B. elegans?) by Kühner (5) and the three examulate species presented above. In each case, the development is pseudoangiocarpic. The same is probably true of the annulate B. subluteus Peck. In the few young stages of this species studied by the present writers, every feature is similar to what has been found for comparable stages of the four species just mentioned, except of course for the lack

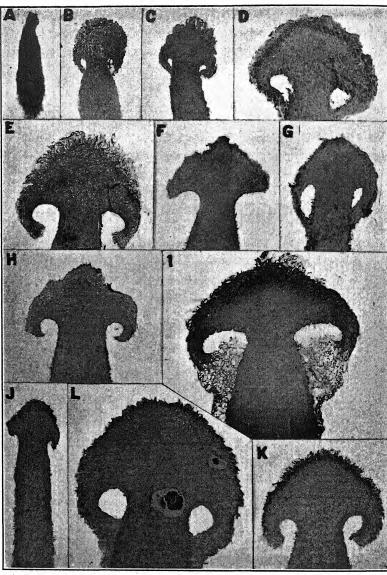


Fig. 2. A-E, Boletus granulatus: A, entire carpophore,  $240 \,\mu$  broad at tip,  $\times$  20; B,  $560 \,\mu$  stage, with marginal hyphae barely in contact with the stipe,  $\times$  20; C,  $800 \,\mu$  stage, with margin in contact with stipe and the hymenial cavity closed,  $\times$  20; D, 1.7 mm. stage, with pileus expanding but the margin still in contact with the stipe,  $\times$  20; E, 2.4 mm. stage with the margin pulled away from the stipe,  $\times$  15. F-H, Boletus americanus: F, early stage, 1.2 mm. broad, before the margin begins to incurve,  $\times$  23; G,

of annulus in three of them. It would appear that Kühner's statement (*loc. cit.*) that all annulate species of the Viscipelles probably develop pseudoangiocarpically could be modified to include *all* species of this group (or genus), annulate or examulate.

## BOLETINUS SPECTABILIS AND B. PICTUS

In small specimens of *Boletinus spectabilis* 800  $\mu$  broad, 4 mm. tall (FIG. 2, J), the pileus has already taken shape, with the hairy margin curved toward the stipe. The surface consists of a trichoderm of coarse, septate filaments 80  $\mu$  long on the disc and progressively shorter toward the margin. The margin soon becomes hairy-tomentose, but the formation of scales does not take place until the pileus is 3 mm. broad.

In the youngest stages, the stipe is progressively more hairy-tomentose downward, but very shortly it becomes more hairy upward, especially as the margin approaches, and finally makes contact with, the stipe.

The hymenial region begins to be compacted in carpophores  $900 \,\mu$  broad. In stages 1.4 to 1.5 mm. broad, a palisade with cystidia and spore-forming basidia is present on the upper stipe, and with little more enlargement of the pileus (1.6 mm. stages, Fig. 2, K), cystidia and basidia are present to the top of the hymenophore arch (midway to the margin). The entire hymenial area is not fertile until about the 3 mm. stage, and even then the cystidia and mature basidia are few.

As has been implied, the pileus expands in a gymnocarpic manner, with the margin becoming hairy and curving toward the stipe before the pileus is  $400 \,\mu$  broad. The hymenium is mature on the stipe (at about 1.5 mm. stage) before the margin makes contact with the stipe. This incurving continues, and contact is

<sup>1.5</sup> mm. stage, with the margin in contact with the stipe and the hymenial cavity closed, showing black-stained viscous material on the margin,  $\times$  15; H, 1.7 mm. stage, with the margin retracted and the hymenial cavity open,  $\times$  18; I, Boletinus pictus, 4 mm. stage, with thick marginal, wad-like veil,  $\times$  12. J-L, Boletinus spectabilis: I, 800  $\mu$  stage, with beginning of incurving of margin toward stipe,  $\times$  20; K, 1.6 mm. stage, with the margin incurving toward the stipe,  $\times$  20; L, 3.2 mm. stage, with the margin in contact with the stipe; two cavities made by larvae are present, with a cross-section of a larva in one cavity and larval pellets containing ingested spores in both cavities;  $\times$  14.

sometimes made as early as the 1.4 mm. stage, at which time the hymenium is mature and producing spores on the upper portion of the stipe. On the other hand, contact of the margin with the stipe is often not made until about the 3 mm. stage, when the hymenium is mature all the way to the margin. Hence, it may be seen that the basidia are producing spores on the stipe at least as soon as the cavity is closed, and in some, if not in most, cases, it may be fertile all over before closure takes place. The least that can be said is that the hymenium is often fertile over much of the area before the cavity is closed by the incurving margin, although the folding of the hymenophore to form the tubes does not take place until after closure.

The beginning of the formation of the hymenium is therefore external in origin or gymnocarpic, and much of the early development may be so, but the carpophore soon becomes angiocarpic (FIG. 2, L), and remains so until the veil parts to form the annulus when the pileus is about 5 cm. broad. Accordingly, this species is pseudoangiocarpic, like *Boletus flavus* (5) and *Boletinus cavipes* (6), at least in Kühner's sense and unless one places the emphasis upon the early and incomplete maturing of the hymenium and the first spore production.

In the smallest stages of *Boletinus pictus* available (1 mm.), the entire carpophore is covered with a loose trichoderm which is rather sharply distinguishable from the flesh of the stipe but not at all so from the flesh of the pileus, and which forms a thick wad at the point where the margin touches the stipe. In 3 to 4 mm. stages, this layer of more or less erect hyphae becomes recumbent from the disc toward the margin and tends to become pulled apart and matted into scales, which are more or less definite at about the 6 to 7 mm. stages.

The marginal hyphae are in contact with the stipe in the 1 mm. stage. The margin begins to pull away when the pileus is about 3 mm. broad, but the hyphal complex which will form the veil and the annulus is a thick wad of tomentum. This becomes thicker instead of thinner and pretty well fills the hymenial cavity until the pileus becomes 15–16 mm. broad. Only then does it begin to stretch and to form a thin, velar membrane. The veil often does

not part from the margin of the pileus until the latter is nearly 4 cm. broad.

The hymenophore of B. pictus is first evident as a compacting of the tissue about the 2 mm. stage and a palisade is evident at about the 3 mm. stage, with cystidia and spore-bearing basidia on the upper part of the stipe and with cystidia on the top of the arch halfway to the margin. At about 3.5 mm., the hymenophore begins to fold. At the 4.5 mm. stage (FIG. 2, I), the hymenium is well folded in the cavity and extends down the stipe well below the attachment of the marginal hairs of the developing veil. At the 6.5 to 7 mm. stages, the hymenium on the stipe begins to break up and the elements become laid flat to form a sort of pseudocutis. The tubes are about 1.5 mm. long on the 17 mm. stage.

It is evident that the hymenium *develops* angiocarpically, but with no stages smaller than 1 mm. available, it is not at present known whether the earliest phases of hymenium development are gymnocarpic as in *B. spectabilis* (and hence of the pseudoangiocarpic type in general), or completely angiocarpic.

The annulus of both *Boletinus spectabilis* and *B. pictus* is obviously peripileic in origin.

## SUMMARY

Ontogenetic studies were made of five species of Boletaceae: three exannulate species with glandular-dotted stipe of the Viscipelles of Boletus (genus Ixocomus of the Europeans)—B. placidus, B. granulatus and B. americanus; two species of Boletinus—B. spectabilis and B. pictus.

The development of *Boletus placidus*, *B. granulatus* and *B. americanus* is fundamentally the same. The hymenium first forms gymnocarpically upon the apex of the stipe; the hairy margin of the pileus gradually incurves to make contact with the stipe as hymenial development continues centrifugally; and the margin later pulls away without leaving any semblance of annular material on the stipe. These three species are therefore all pseudoangiocarpic in Kühner's sense. As far as is known, this is the first report of pseudoangiocarpy in exannulate Boleti.

The annulate *Boletinus spectabilis* develops similarly and is likewise pseudoangiocarpic.

Boletinus pictus, likewise annulate, probably develops in a manner entirely similar to *B. spectabilis*, and is probably pseudoangio-carpic, but this cannot be stated certainly because the very earliest stages of the carpophore were not available.

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# A STUDY OF SEXUALITY IN SAPROMYCES REINSCHII<sup>1</sup>

HARLOW BISHOP
(WITH 6 FIGURES)

In the studies of sexuality in the lower fungi the pioneer work of Blakeslee (2, 3, 4) on the Mucorales was of especial significance since for the first time it demonstrated by experiment that in these Zygomycetes there were two distinct types of sexuality. In one, which he named homothallic, the individual mycelium (plant) comprised both sexes so that on it conjugation and the formation of zygotes regularly took place. In the other, which he named heterothallic, an individual mycelium was of one sex only, either pure male (minus), or pure female (plus), and therefore mating with a mycelium of the opposite sex was necessary for sexual reproduction. So clear cut and definite were these sexual conditions established by Blakeslee and so effective was his experimental approach that subsequent investigations in the whole field of sexuality in the lower plants were notably stimulated and influenced. Kniep (17) has effectively summarized the progress of this investigation up to 1929 and has pointed out the need for further study.

In another phycomycetous group, the Oömycetes, heterothallism was demonstrated by Couch (13) in 1926 in *Dictyuchus monosporus* Leitgeb, a member of the Saprolegniaceae. One of Couch's female strains, however, was remarkable for its possession of latent male potentialities. Another significant contribution was the discovery by Raper (22) in *Achlya bisexualis* Coker, of three types of sexual strains, male, female and hermaphroditic-female. Studies in the Saprolegniaceae, therefore, indicate a more complex type of sexuality than has been thus far observed in the Mucoraceae.

In another Oömycete, Sapromyces Reinschii (Schroeter)

<sup>&</sup>lt;sup>1</sup> Contribution from the Laboratories of Cryptogamic Botany and the Farlow Herbarium, Harvard University, No. 155.

Fritsch, preliminary work by Jordan in 1927 (Weston, 26) had shown a seemingly heterothallic condition. This species, one of the Leptomitaceae, had been selected by Weston as especially suitable for a study of sexuality because its sex organs are highly differentiated and distinctive, the oögonia large and easily recognized, the antheridial branches well developed and sharply defined, while the zoöspores are uninucleate and therefore permit "isolation and the determining of sex potentialities without the possible complications of the heterocaryotic mingling of nuclei of different sexes which might handicap such studies in the Mucorales." Moreover, Sapromyces, as a member of the Leptomitaceae, offers an opportunity to compare the sexuality of this family with that found in Dictyuchus of the Saprolegniaceae.

An investigation of the sexuality of Sapromyces was undertaken by the writer in 1933 and although impeded by heavy schedules of teaching has been carried on ever since. The purpose of the work was to study intensively the sexual manifestations of mycelia derived from single zoöspores and hence interpretable from the standpoint of the sexual potentialities of a single nucleus. The results are presented in the following pages.

# MATERIALS AND METHODS

Of eight source collections, number 5, obtained by Dr. A. G. Kevorkian in June 1933 from a sphagnum bog near Walpole, Mass., and number 7, obtained by the writer in June 1935 from a sphagnum bog near Laurelton, N. J., at the approximate location of P. H. Jordan's collections in 1926–1927 (Weston, 26), showed in the original cultures the characteristic sexual reproduction which readily distinguished the material as Sapromyces Reinschii (Schroeter) Fritsch. This species has recently been reduced by Coker (11) to synomymy under S. elongatus but the inadequacy of Cornu's (12) characterization of Rhipidium elongatum in 1872 compared with the completeness of Thaxter's (24) detailed description of S. Reinschii in 1894 seems to give doubtful basis for the change. The writer therefore retains the name S. Reinschii in the present paper.

The remaining six collections developed abundant zoöspores but, as in the so-called "sterile" material studied by Coker (9, 10) and others, formed no sex organs in the original cultures.

As any exacting study of the sexual situation in a water mold such as this demands that pure cultures be derived from single zoöspores and grown on artificial media under controlled conditions, considerable time was spent in meeting these requirements.

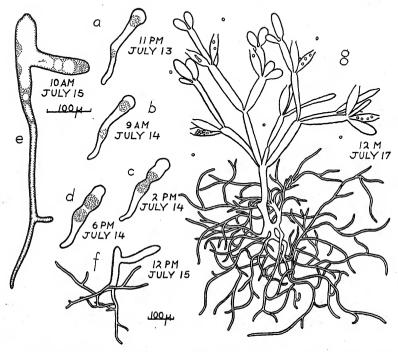


Fig. 1. Drawings showing successive stages in the development in pure culture of a single germinated zoöspore a into a mature plantlet g. From camera lucida drawings, magnification of a-e, upper scale, of f-g, lower scale.

Pure cultures from single zoöspores were obtained in two ways. In the first, from zoöspores discharged in hanging drops by repeatedly washed sporangia, young sporelings with short sturdy germ tubes were picked out with a micropipette in a Barber (1) manipulator and transferred to successive drops of sterile water until presumably free from bacteria. These selected sporelings were then transferred to drops of 2 per cent peptone solution where a satisfactory percentage of them, uncontaminated, developed in four days into vigorous plantlets with rhizoids, main axes and sporangium-bearing branches, as shown in figure 1.

As these grew larger (Fig. 1, g) and became visible to the unaided eye they were removed with fine forceps and planted on suitable nutrient agar in petri dishes.

In the second method, repeated isolations of vigorous hyphal tips from successive mycelia growing on prune agar and on corn meal agar finally resulted in pure mycelial cultures. These were easily induced to produce sporangia and discharge zoöspores which were picked out singly with the Barber micropipette and used to start single spore pure cultures on nutrient agar.

Twenty-three mycelial pure cultures were isolated from the sexually reproductive collections 5 and 7. From the four most vigorous and promising of these mycelia 154 single spore isolations were made, of which 37 were successfully brought to maturity to serve as stock cultures for subsequent investigation. Two more single spore cultures, isolated directly from collections 1 and 5, were successfully established. The following table (Table I)

TABLE I
ORIGIN OF THE 39 SINGLE SPORE STRAINS

Parent mycelia	Single spore strains	Totals
Sapromyces 1	Sapromyces 1C	1
Sapromyces 5	Sapromyces 5B	1
Sapromyces 5-4	Sapromyces 5T, 5W, 5X, 5L3, 5M3, 5N3, 5V3, 5W3, 5Z3, 5A4, 5C4, 5F4, 5F4-A, 5F4-B, 5J4, 5L4	16
Sapromyces 5-5-3	5-5-3 Sapromyces 5T4, 5X4, 5X4-D-B, 5Y4, 5Y4-G, 5Y4-H, 5Y4-I, 5Y4-J, 5Z4	
Sapromyces 5-5-1	Sapromyces 5T5, 5U5, 5W5	3
Sapromyces 7-1-1	Sapromyces 7A, 7A-B, 7A-C, 7B, 7C, 7D, 7E, 7F, 7G	9

lists the sources of these 39 single spore strains, the original gross cultures being numbered 1, 2, etc., the first mycelial isolates being numbered 5–1, 7–2, etc., subsequent mycelial isolations from these 5–1–1, 5–1–2, etc., the final single spore cultures being designated by A to Z, A2 to Z2, and so on, in the order of isolation from each gross collection and without reference to the particular my-

celial partition of a gross collection (e.g. Sapromyces 1C was the third single spore culture isolated from gross collection 1 while Sapromyces 5T4 was the 98th single spore culture isolated from gross collection 5).

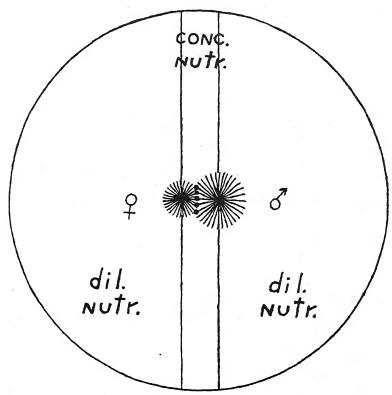


Fig. 2. Schematic diagram showing method of mating  $\delta$  and  $\mathfrak P$  strains in pure culture on nutrient agar in Petri dishes. The  $\delta$  and  $\mathfrak P$  mycelia, starting in dilute nutrient, grow across the median strip of concentrated nutrient, intermingle and develop sex organs. Mag.  $\times$  1.

Pure culture on artificial nutrient media is obviously essential in studying the sexual situation in a fungus such as this. Yet before the present investigation, no species of Sapromyces had ever been grown successfully thus even though von Minden (20) had cultured the related genera Araiospora and Rhipidium in his study of their development. The method used by Jordan (26) and by Kevorkian (16) of growing Sapromyces on barberries in

water cultures supported sexual reproduction and proved useful within its obvious limitations. The writer early in this investigation successfully grew *S. Reinschii* in pure culture on prune agar and corn meal agar but, on these media, although mycelial growth was satisfactory and numerous antheridial branches were produced the development of oögonia was sparse and inconsistent.

In seeking a synthetic medium which would induce the formation of abundant sex organs with certainty, the chemical analyses of barberries (19), prunes (27) and corn meal (28) were examined for the important nutrients common to them. It was concluded that a combination of dextrose or levulose (or both), globulin or the more easily secured proteose peptone, and such small amounts of the elements Mg, P, K, and S as are contained in Knop's solution, a mixture of the same general type as the Brown and Lipman's nitrate peptone agar of Levine and Schoenlein (18), should prove suitable. Accordingly several such combinations were tested and of these two proved especially successful; nutrient 1, comprising levulose 2 per cent, dextrose (anhydrous) 2 per cent, proteose-peptone 1 per cent, Knop's solution 0.1 per cent, agar 1 per cent, with glass-distilled water, and nutrient 2, the same save that the levulose was omitted. On medium 1, undiluted, both male and female strains produced dense mycelial growth but when mated neither produced sex organs since nutrient concentration of 6 per cent or higher of the three principal ingredients gave vegetative development only. On nutrient 2, both when male and female strains were mated and when they were grown separately under identical conditions, growth of the male mycelium was accelerated, of the female decelerated as is strikingly shown in figure 6, a and b, of mycelia grown in separate dishes.

Since neither these media nor their modifications were alone successful in inducing abundant and consistent production of sex organs, various combinations were tried and finally the following procedure was found to be effective. A strip of glass, one-quarter inches wide, slightly less in length than the diameter of a petri dish and of about the thickness of the layer of agar to be used, was placed flat on the bottom of a dry petri dish and the whole was sterilized. *Sapromyces* agar "1," of 1/10 dilution, but containing 1 per cent agar so as not to interfere with the hardening

qualities, was poured on the right and left sides of the glass strip and allowed to cool. The glass strip was then removed and undiluted *Sapromyces* agar "1" was poured into the slot so left. After the cooling of the entire medium, a male strain was planted at one margin of the undiluted agar and a female strain at the other margin. Within ten days the female strain formed a dense mass of oögonia and the male strain a great number of antheridial branches at the points of contact within the undiluted agar (Fig. 2).

Extensive observations of male and female strains, mated by this method, showed that functional oögonia and antheridia were formed abundantly, fertilization took place and normal oöspores were matured. Hence this method was used for most of the experimental work which follows.

#### EXPERIMENTAL WORK

#### EXPERIMENTS TO IDENTIFY SEXUAL STRAINS

The sexual identity of the 39 strains studied by the writer was at first unknown, because they had originated from single zoöspores whose derivation could not be traced with the certainty of the isolated basal cells used by Jordan in establishing the apparent heterothallism in this species.

Very early in the study, however, it became apparent that the strains fell into two groups on the basis of rate of growth of the mycelium, one group growing with noticeably greater rapidity, the other distinctly more slowly. From the findings of Blakeslee and others in their work on the Mucorales, the strains growing more rapidly would be expected to be plus or female. Yet close examination of these strains showed that frequently they produced short, slender outgrowths resembling antheridial branches (FIG. 3b). They were therefore considered to be probable male strains. The other less rapidly growing group of cultures never produced outgrowths resembling antheridial branches but did, on rare occasions, develop peculiar, repeatedly proliferated structures which seemed to be abortive oögonia (FIG. 3g). Consequently the latter strains were considered as probable females.

On the basis of the above observations ten strains (5T, 5W, 5W3, 5Z3, 5C4, 5J4, 5L4, 5T4, 5Y4, and 5Z4) were grown simul-

taneously on separate dishes of prune agar so that their growth rates could be compared. Only ten strains were tested in these early experiments since at that time only about one-half the total 39 single spore strains had been isolated. Four of these ten strains (5T. 5W3, 5Z3 and 5J4) extended 2.5 to 4.0 cm. in diameter in ten days and consistently produced outgrowths resembling antheridial branches while the other six (5W, 5C4, 5L4, 5T4, 5Y4 and 5Z4) spread only 1.0 to 2.2 cm. and one of these (5Y4) developed structures resembling oögonial initials. From these indications, strains 5T, 5W3, 5Z3 and 5J4 were tentatively considered male, and strains 5W, 5C4, 5L4, 5T4, 5Y4 and 5Z4 were tentatively considered female, and the strains of one group were mated on corn meal agar in all possible combinations with the strains of the other group. The results of these preliminary matings are shown in the following table, 0 indicating no sexual reaction and d ♀ indicating a sexual reaction with the strain from the left hand column forming antheridial branches, the opposing strain (top column) oögonia.

TABLE II
SEXUAL REACTIONS IN THE FIRST 24 MATINGS

	5W	5C4	5L4	5 <b>T</b> 4	5Y4	5Z4
5T 5W3 5Z3 5J4	0 0 0	0 0 0 ♂ 0	0 0 0	7 P 7 P 7 P	\$\$\$\$\$	0 0 0

It is of interest to note that in these matings the supposed male strains of the left column all consistently corroborated the tentative diagnosis as male, while of the supposed female strains in the top column, 5Y4 behaved consistently as female in each mating while 5T4 behaved consistently as female in three of the matings, even though in the fourth, with 5Z3, it failed to form oögonia.

In later experiments with the doubtful strains, 5W, 5C4, 5L4 and 5Z4, two of these, 5W and 5L4, proved to be neutral or neuter, since they never produced any sex organs, 5C4 proved to be practically neutral although on one other occasion it again de-

veloped antheridial branches, while 5Z4 proved to be female with the same sexual behavior as 5Y4 and 5T4, although so lacking in vegetative vigor that it became more and more feeble and eventually died.

Thus, of the first ten strains critically examined, 5T, 5W3, 5Z3, 5C4 and 5J4 were found to be male, 5T4, 5Y4 and 5Z4 female, and 5W and 5L4 neuter or neutral strains. Apparently a rough but serviceable means of diagnosis was afforded by the two criteria, a the rate of growth, more rapid in the male than in the female mycelia, and b the development of recognizable initials of the sexual apparatus, i.e. antheridial branches on the male and oögonial initials or abortive oögonia on the females. By means of these, the sexual character of seven out of ten cases was correctly determined, all four of the male strains, 5T, 5W3, 5Z3 and 5J4, were correctly predicted as male and the three female strains, 5T4, 5Y4 and 5Z4, as female. The two sterile strains, 5W and 5L4, and the single, weak male strain, 5C4, were erroneously predicted as female.

The strongly male and strongly female strains determined by these preliminary pairings were used in subsequent matings as the basis for identifying the sexual character of additional strains. The sexual nature of the individual isolates was not determined for all of the 39 strains but repeated tests and numerous pairings in suitable combinations revealed the character of the 17 strains most intensively studied to be that shown in the following table.

TABLE III
SEXUALITY OF THE 17 STRAINS MOST STUDIED

Strongly	Weakly	Neutral	Weakly fe-	Strongly fe-
male strains	male strains	strains	male strains	male strains
5T 5W3 5Z3 5J4	5C4	5W 5X 5A4 5F4 5L4	5Z4	5T4 5X4 5Y4 5T5 5U5 5W5

The present investigation concentrated chiefly on the more strongly sexed of these strains in the hope that an understanding of their behavior may help toward interpreting the nature of the less well defined weakly sexed strains which the writer plans to study further in the future.

## MANIFESTATIONS OF SEX-GENERAL FEATURES

The distinction of male and female strains on the basis of mycelial growth being more rapid and vigorous in the male, less in the female, used in preliminary identification was found on

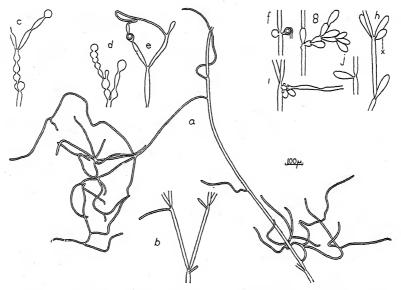


Fig. 3. Drawings showing reproductive structures developed under various conditions: a, antheridial branches of degree V formed by d 5T mated with  $\mathcal{P}$  5T5; b, antheridial branch initials formed by d 5T growing alone; c and d, proliferated and aborted obgonial initials (not reached by antheridial branches) formed by  $\mathcal{P}$  5T5 mated with d 5T; e, hermaphroditic selffertilization in  $\mathcal{P}$  5T5 mated with d 5T; f-j, sex organs of  $\mathcal{P}$  5T4 growing alone, f, hermaphroditic self-fertilization, g-j, abortive organs. From camera lucida drawings, magnification according to the scale.

further investigation to be an even more valid and significant criterion than had at first been appreciated. Tests of various media showed that some emphasized this difference very markedly, one of these, *Sapromyces* agar 2, described above, accentuating the difference of mycelial growth so that the growth of the male mycelium in diameter was five times more rapid than that of the

female as is well shown by figure 6a of the Q mycelium and 6b of the Q after one month's growth under identical conditions.

The fact that in *Sapromyces* growth of the male strains is consistently and markedly more vigorous and rapid than that of the female is of interest as a helpful criterion of distinction between the two and because, being exactly the reverse of what Blakeslee found in the Mucorales, it casts additional light on the manifestations of sex in the lower plants.

Repeated observations revealed that the first signs of sexual reproduction consistently appeared in a zone below the apex of the segments of male and female thalli. In this zone, just below the extreme tip where the zoösporangia and vegetative segments arise, originate the first antheridial branches and oögonial initials recognizable even at early stages by their more proximal position and by the fact that they grow out more nearly at right angles. In the case of male plants the first antheridial branches appeared in this zone (FIG. 3b) while in response to minimal stimulation later antheridial branches also originated here although under greater stimulation they might develop at almost any point along the hyphal segments (FIG. 3a). In the female plants the oögonial initials (FIGS. 3h, i, j) usually developed in this zone under any degree of stimulation. This sub-apical area of the segment, therefore, seems to be a critical point for the formation of sex organs.

After the formation of the initials has begun the further development and maturation of the sex organs in suitably mated cultures follows a regular and well defined course. This, as is illustrated in figure 4 by four successive drawings from a complete series of camera lucida sketches of a mating of 5J43 with 5T52, involves the growth of the antheridial branch (FIG. 4a, b), its contact with the organial initial (FIG. 4c), the delimitation of antheridium and organium with fertilization by means of a fertilization tube and the maturation of a single organic (FIG. 4d). Measurements based on these drawings and on others equally typical show that the antheridial branch grew in length an average of  $105~\mu$  an hour while the organium increased in diameter an average of  $4.2~\mu$  an hour.

One interesting phenomenon observed repeatedly in these matings of  $\beta$  and  $\beta$  plants was the production of antheridial branches

by the males before any contact between the  $\mathcal{J}$  and  $\mathcal{L}$  mycelia. In matings in Petri dishes on such nutrients as corn meal agar or Sapromyces 1 agar with the  $\mathcal{J}$  and  $\mathcal{L}$  mycelia growing out from inoculation centers 2 to 2.5 cm. apart the  $\mathcal{J}$  plants developed antheridial branches of degree II, III or even IV (as explained later) some time before any actual contact between the approaching fringes of the mycelia. Moreover the development of antheridial branches was more extensive (degree IV) and more abundant on that part of the  $\mathcal{J}$  mycelium nearest the  $\mathcal{L}$  and decreased down to sparse (degree I) and scant development on the opposite side of the  $\mathcal{J}$  mycelium farthest from the  $\mathcal{L}$ . This would seem to indicate that from the  $\mathcal{L}$  mycelium there diffuses some substance, probably a hormone, which stimulates the formation of antheridial branches by the male.

The writer, therefore, attempted under more controlled experimental conditions to secure more positive evidence for the production of such a substance by the female plants. A strongly ♀ strain 5T5 and a strongly ♂ strain 5J4 were grown on barberries in sterile water cultures in separate flasks and, after two weeks growth had covered the bottom of each flask with dense mycelial tufts, the liquid of each was filtered off through a Berkefeld filter. Meanwhile 12 Petri dish cultures had been prepared, 6 containing vigorous 4 days old 2 mycelia of 5T5 growing on corn meal agar and 6 containing similar of mycelia of 5J4. To these cultures the filtrate was added as follows: of the filtrate from the 95T5, 1 cc. was poured over the 3 mycelium 5J4 in each of 2 Petri dishes, 1/2 cc. was poured over the 3 mycelium 5 J4 in 2 dishes and 1 cc. was poured over the 2 mycelium 5T5 in 2 dishes. In like manner, of the filtrate from the 3 5J4, 1 cc. each was added to 2 dishes of the Q 5T5, 1/2 cc. to 2 dishes of the Q 5T5 and 1 cc. to 2 dishes of the 3514.

The  $\mathcal{J}$  mycelia in the 4 dishes to which  $\mathcal{Q}$  filtrate had been added in amounts of 1 cc. and of 1/2 cc. began to develop antheridial branches after 2 days. Attempts to evaluate this reaction in quantitative terms were not very satisfactory but, as a sample, an examination of 100 hyphae selected at random in a strip across the  $\mathcal{J}$  mycelium to which 1 cc. of  $\mathcal{Q}$  filtrate had been added showed, after 17 days, 85 hyphae with no reaction, 7 with antheridial

branches of degree I, and 8 with antheridial branches of degree II. Yet qualitatively the experiment gave evidence for the production by the  $\mathfrak P$  of such a substance for the  $\mathfrak P$  filtrate did stimulate antheridial branch formation by the  $\mathcal P$  while in all the other plates with  $\mathfrak P$  filtrate added to  $\mathfrak P$  mycelium,  $\mathcal P$  filtrate added to  $\mathfrak P$  mycelium, no sexual reactions occurred.

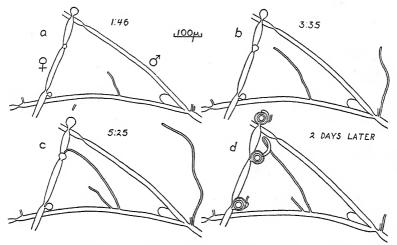


Fig. 4. Drawings showing successive stages in the formation of sex organs in a mating of 5J4  $\delta$  and 5T5 9 (under culture conditions of figure 2). Note the directional growth of the antheridial branch. From camera lucida drawings, magnification according to scale.

Another interesting phenomenon observed in matings between strongly 3 and 2 strains was that the antheridial branches, although somewhat sinuous rather than straight, in general appeared to grow directly toward the oögonia and, when very close, to curve precisely to attach at the very apex or distal pole of the oögonial initial (FIGS. 4, 5). Many such observations seemed to indicate that there is some definite stimulus operating to bring the antheridial branch into actual contact with the öogonium. A typical example of this phenomenon is shown in figure 6i in which one antheridial branch of the male strain has already made contact with an oögonium of the female strain and has developed an antheridium while three other antheridial branches can be clearly seen, their tips forming an arc of approximately 90 degrees, ac-

curately pointing toward the same oögonium. Many such observations seemed to indicate that the growth of the antheridial branches toward the oögonia was influenced by the diffusion of some substance from these.

The foregoing observations, although preliminary and not adequately verified by controlled experiments, seemed to justify the assumptions that some substance diffusing from the  $\mathcal Q$  mycelium stimulated the development of antheridial branches on the  $\mathcal Q$  and that these in turn were influenced to grow directly toward the oögonia by some substance diffusing from the oögonia themselves. These assumptions seem now to be established beyond doubt by the masterly work of Raper (23) on the rôle of hormones in the sexual reproduction of *Achlya bisexualis*.

## MANIFESTATIONS OF SEX IN MALE STRAINS

The primary manifestation of sex in the male strains, namely the formation of antheridial branches, shows marked differences in degree under different conditions and in various strains. When growing by themselves on corn meal agar strongly sexed male strains always, and weakly sexed usually, form antheridial branches. These are usually short and invariably lack constrictions and secondary branches. When mated with strongly female strains on corn meal agar the vigorous male strains develop numerous antheridial axes which are of considerable length (equal to 20 hyphal segments or more) with many constrictions and abundant dense branches. Between these two extremes there are various intermediates so that it is necessary to designate by arbitrary symbols the degree of sexual response manifested. Symbol 0 denotes that antheridial branches are lacking, I that they are present but short and simple, II that they are long and simple, III that they are very long with numerous nodal constrictions, IV that they are sparingly branched, V that they are densely branched.

Whatever their degree the antheridial branches are readily distinguished from rhizoidal outgrowths. Branches arising at the critical point for sex organ formation in the zone just below the segment apex are, of course, easily distinguished by their position. Even antheridial branches arising elsewhere can be identified by their approximately uniform diameter in contrast to the tapering

of rhizoids and if of great length and profuse branching the additional feature of occasional constrictions, serving as regions of origin for the secondary branches, distinguish them from the lack of constrictions and haphazard branching of the rhizoids.

The typical behavior of strongly male strains is well exemplified by reactions of *Sapromyces* 5T. When grown alone on such media as corn meal agar or Difco prune agar this strain shows great mycelial vigor, develops abundant zoösporangia and forms small antheridial branch initials of degree I (FIG. 3b). When mated with strongly female strains such as 5T5 on such substrata the male develops very abundant extensive antheridial branches of degree V (FIG. 3a), these being so numerous and so densely matted that they can be recognized, even by the unaided eye, as a conspicuous, fine, dense turf. When mated under more natural aquatic conditions in water cultures on such substrata as barberries the male forms abundant antheridial branches of degree IV and these coming in contact with the numerous oögonia developing on the female, attach and form normal functional antheridia which accomplish fertilization.

The other strongly male strains investigated (see Table III) showed essentially the same behavior.

# MANIFESTATIONS OF SEX IN FEMALE STRAINS

The typical behavior of a strongly female strain is shown by Sapromyces 5Y4. When grown alone on prune agar this strain develops a relatively weak mycelium with very few zoösporangia, and forms abortive oögonia occasionally and normal oögonia very rarely while on corn meal agar it commonly develops abortive oögonia and occasionally normal oögonia. In matings with strongly male strains on suitable media this strain usually produces oögonia in abundance, although occasionally few if any are formed. When, for example, this strongly female strain 5Y4 is mated on corn meal agar with the strongly male 5J4 the female develops numerous oögonia to which the antheridial branches from the male extend and the antheridium attaches to accomplish fertilization (FIG. 5a, b). When such strongly sexed strains are mated on a narrow strip of agar 1 surrounded by diluted agar (cf. Methods, Page 506) abundant production of sex organs takes place, the  $\mathfrak Q$  form-

ing dense crowds of oögonia which are consistently furnished with antheridia developed by the accompanying  $\mathcal{J}$  as is illustrated by figures 6d and 6g in the case of strongly  $\mathcal{D}$  5T5 with strongly  $\mathcal{J}$  5J4. When strongly female strains are mated with strong males

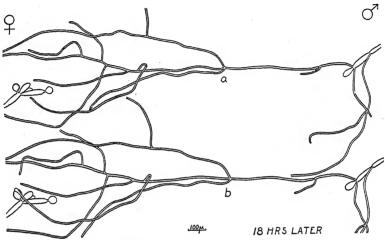


Fig. 5. Successive stages in a mating of  $\delta$  5J4 and  $\mathfrak P$  5Y4 on corn meal agar showing in a, the directional growth of antheridial branches toward the objection and in b, the contact, attachment and beginning of antheridium formation by one  $\delta$  branch. From a series of camera lucida drawings, magnification according to scale.

under the more natural aquatic conditions of growth on barberries in water cultures the formation of oögonia is more profuse than on any agar medium; so abundant that it reveals itself by a dense dotting visible even under a hand lens.

Perhaps the most interesting and significant point observed in this study of sex manifestations was that the female strains, in addition to oögonia, are able to produce antheridial branches and functional antheridia. This unexpected phenomenon occurs fairly commonly in female strains grown alone in separate culture and is apparently influenced to some extent by the substratum. When grown alone on corn meal agar or prune agar, for example, the females were found to form not only oögonia but also antheridial branches (FIG. 3f) which applied their tips to the oögonia and developed antheridia which were seemingly functional and accomplished fertilization as these oögonia developed normal mature

oöspores. In such pure cultures of females alone there could be no doubt that the antheridial branches arose from the female even though their point of origin was at such a distance from the antheridium and the oögonium to which it was attached that the course of the antheridial branch could not be traced with certainty to its source. Similarly when female strains were grown alone on barberries under the more natural conditions of water cultures these females developed not only oögonial initials but also antheridial branches and functional antheridia. Although these were slower in developing (after three weeks) and fewer in number their presence was confirmed by careful examination in numerous cultures of this kind.

When vigorous females were mated with strongly male strains on such media as a mixture of corn meal agar and half strength prune agar there occurred, in the zone of intermingling, the usual procedure of mating and fertilization as already described, the female developing abundant oögonia of which practically all are furnished with antheridia originating from the opposing male. Just outside of this zone of intermingling, however, the female not reached by antheridial branches from the male may show repeated proliferation of oögonial initials (FIG. 3c, d) with the formation of antheridial branches from the female itself. In such cases the antheridial branches originated at some distance and while in some instances it was possible to trace the antheridial branch to its origin on the female plant as much as 15 hyphal segments away, in other instances the antheridial branches were of such distant origin that their source could not be ascertained with certainty. In a few cases, however, the female developed antheridial branches so near the oögonium that the growth of the d branch to the oögonium, the attachment of the antheridium and the subsequent fertilization of the oöspore could be followed with certainty. Such a case is shown in figure 3e where the condition of hermaphroditism with self-fertilization is obvious and somewhat resembles the androgynous condition in Thaxter's Sapromyces androgynus (25).

When similar matings were grown on strips of *Sapromyces* agar 1, surrounded by the same but diluted agar, the females were never observed to develop antheridial branches.

In none of the preceding cases did the females develop antheridial branches alone without the coincident formation of oögonia.

The foregoing instances of sexual behavior in the female strains of *Sapromyces*, involving not only the hermaphroditic production of antheridial branches but even self-fertilization, thereby in a manner comparable to homothallism in Blakeslee's sense of the term, is so different from heterothallism that it seems necessary to state that these observations were corroborated repeatedly and that all the precautions against contamination or mixing of strains emphasized by Blakeslee (5) as essential in the Mucorales were taken in the present work.

#### DISCUSSION

In order to evaluate the possible significance of the sexual condition in Sapromyces Reinschii, which this study has revealed, it is necessary to consider the chief theories for the interpretation of sexuality in the lower plants. Of these two are especially significant, the homothallism vs. heterothallism concept first formulated by Blakeslee (2, 3, 4) in the Mucorales and since elaborated and extended by other investigators (8), and the theory of relative sexuality formulated by Hartmann (14, 15) from work on the algae and since extended to other groups. Heterothallism implies strict unisexuality of individuals and while both plus 2 and minus d strains may show notable range in degree of sexual vigor (6, 7) no evidence for true sexual intergrades has been adduced. The temporarily bisexual condition in mycelia resulting from zygospore germination in forms with delayed segregation such as Phycomyces (3) or resulting from the artificial myxochimaeras produced by Burgeff (8) may be interpreted as instances of heterocaryosis in Burgeff's sense, the individual nuclei of the coenocytic multinucleate mycelium or of the 6 to 11 nucleate sporangial spores possibly being each of only one sexual potentiality, either plus or minus, and their relative proportions controlling the resulting sexual reactions.

Relative sexuality on the other hand postulates, even in single nuclei, male potencies (A) and female potencies (G) under the control of male realisators (alpha) and female realisators (gamma). In the male strain of haplogenotypic, heterothallic

organisms, the male realisator (alpha) is at once the means of activation of the male potency (A) and the inhibition of the female potency (G). The reverse is true in the female strains of such organisms, where the female realisator (gamma) activates the female potency (G) at the expense of the male potency (A). The strength of a given strain in sexual reproduction is termed its valence, which is the equivalent of what Blakeslee terms the "grade" or strength of sexual reaction. Most interesting of Hartmann's results are the rare copulations of strong plus with weak plus strains and of strong minus with weak minus strains. The underlying principle in his theory, then, is that each type of strain, individual, cell and even nucleus, has a bisexual potentiality.

In the light of these two theories it may be profitable to reexamine the instances of so-called "heterothallism" in the Oömycetes. The sexual strains of *Dictyuchus monosporus* studied by Couch (13) behaved as pure males or females with the single exception of strain "N." This female strain was parthenogenetic under ordinary conditions, but germination of one of its parthenogenetic eggs produced a strain which formed antheridia when mated with a strongly female strain. Nagai (21) has discovered in Japan a strain similar to this unusual one of Couch's and considers it sufficiently different to merit specific rank. At least one female strain of *Dictyuchus monosporus* thus harbors a latent maleness, which on rare occasions becomes manifest.

Coker (10) in 1927 described a new species, Achlya bisexualis, which has proved a most interesting case of intersexuality. As since investigated by Raper (22), this species shows the usual male and female strains, but, in addition to these, shows a curious type of strain which Raper has termed hermaphroditic-female. Its characteristics are those of pure female strains except for one feature, namely, the formation of abortive oögonia and undeveloped antheridia when grown alone. Evidently certain strains of this species have a bisexual potency.

The condition in *Sapromyces Reinschii* casts still more light on the problem of sexuality in the Oömycetes. The situation here is roughly comparable to that in *Dictyuchus* and *Achlya*, in which strains are able to form antheridia as well as oögonia. In *Sapro-*

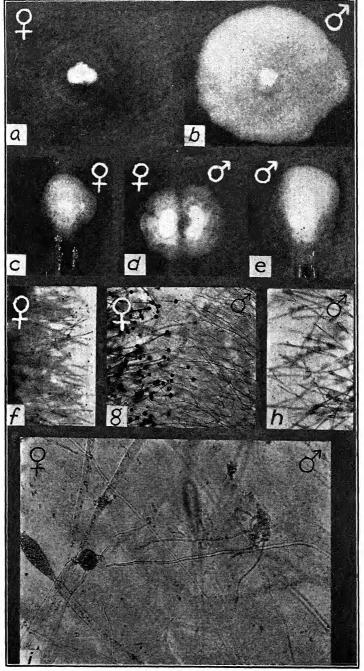


Fig. 6.

myces, however, instead of being a rare condition confined to one or a few female strains, all of the female strains carefully studied have shown that they possess a latent maleness. They may exhibit this phenomenon either when grown alone or even when mated with male strains. In common with Dictyuchus and Achlya the male strains yield only a pure male reaction in every case where they form any sex organs at all. Yet it would seem possible that suitable cultural conditions might induce some of the male strains to form oögonia for it should be remembered that at first, before suitable culture conditions were devised, the writer had great difficulty in inducing even the female strains to produce oögonia. Since all the cultures used for critical experimental work by the writer were derived from single zoöspores, and since Kevorkian (16) has demonstrated the presence of but one nucleus in the zoöspore of Sapromyces Reinschii, Burgeff's theory that each nucleus comprises the potentiality of but one sex would not explain the phenomena observed here. On the contrary the sexual reactions of these female strains indicate that both male and female potentialities are contained in the one nucleus and thus offer additional support for Hartmann's theory of relative sexuality.

Attempting to relate the results of this work with that done on related forms, the writer has formulated a possible interpretation of the sexuality of *Sapromyces Reinschii* involving six conceivable types of strains. It seems justifiable to assume that the pure male strains, symbolized by MM and exemplified by 5T, 5W3, 5Z3, 5C4 and 5J4, may have a theoretical counterpart in pure female strains, symbolized by FF. Predominantly female but latently male strains, symbolized by mF and exemplified by 5T4, 5X4, 5Y4, 5Z4, 5T5, 5U5 and 5W5, may be assumed to have a theo-

Fig. 6. Photographs illustrating typical growth and reproduction of  $\mathcal Q$  and  $\mathcal S$  strains of Sapromyces as exemplified by  $\mathcal Q$  5T5 and  $\mathcal S$  5J4. a and b, photographs  $(\times 1)$  of  $\mathcal Q$  and  $\mathcal S$  mycelia of the same age (one month) grown under the same conditions on agar No. 2 showing the notably more rapid and vigorous growth of the  $\mathcal S$ . c-e, photographs  $(\times \frac{1}{2})$  of  $\mathcal Q$  alone, of  $\mathcal S$  alone, and of  $\mathcal Q$  and  $\mathcal S$  mated growing on agar No. 2 according to the method shown in figure 2. f, g, h, photomicrographs  $(\times 60)$  showing microscopic details of c, d and e respectively. Note the abundant obgonia and antheridial branches in the mated culture g. i, photomicrograph  $(\times 200)$  (from d) showing the directional growth of antheridial branches toward an obgonium.

retical counterpart in predominantly male but latently female strains, symbolized by Mf. Other strains could be postulated in which male and female potentialities are nearly balanced and these might be of two sorts. In one the sexual tendencies could be strong and balanced, symbolized by MF, in the other the sexual tendencies could be weak and balanced, symbolized by mf. The latter type of strain is perhaps exemplified by 5W, 5X, 5A4, 5F4 and 5L4. Both MF and mf types might be expected to be neutral in reaction, because neither sexual tendency would predominate.

If all six types of strains, namely, MM, Mf, MF, mf, mF and FF were to be found, we would have a conveniently codified picture of sexuality in *Sapromyces Reinschii*. Of the six types of strains above postulated, only three, namely, the MM, mf and mF types, have been found as yet. The FF, Mf and MF types appear not to be represented in the strains investigated but it seems possible that collections from additional sources may yield these types. However this may be, the strains of *Sapromyces Reinschii* studied by the writer seem definitely to be of three types: pure males, predominant females with latent maleness, and neutrals.

#### ACKNOWLEDGMENTS

To all those who have helped to make this study possible the writer wishes to express his sincere appreciation. To Dr. William H. Weston, Jr. the deepest gratitude is felt for his suggestion of the problem and for his continued encouragement and stimulating guidance. Thanks are due to Dr. A. G. Kevorkian who supplied the writer with several gross collections of *Sapromyces*, and to Mr. Frank White who made several of the photographs which are here reproduced. While most of the work was done during the summer vacations at the Biological Laboratories of Harvard University, a considerable portion of the work was made possible through the facilities offered by Dr. P. A. Davies of the department of biology of the University of Louisville and through the many courtesies extended by Dr. J. J. Oppenheimer of that institution.

# SUMMARY

- 1. Sapromyces Reinschii from several collections was isolated and grown in pure culture on various substrata, the cultural conditions favoring development of mycelia, zoösporangia and sex organs were worked out and the sexuality studied in detail.
- 2. Thirty-nine pure cultures originating from single zoöspores were raised to mycelial maturity. Of the seventeen isolations studied intensively, four proved to be strongly male, one weakly male, five neuter or neutral, one weakly female and six strongly female.
- 3. The male strains consistently showed more rapid mycelial growth than the female, this difference in growth rate being greatly accentuated on certain media.
- 4. When strongly male and strongly female strains were mated the former developed antheridial branches, the latter oögonia, fertilization occurred and normal oöspores developed.
- 5. Considerable evidence indicated that both the development of antheridial branches on the male and the directional growth of these toward the oögonia were responses to substances diffusing from the female.
- 6. The female strains consistently showed latent maleness and could develop antheridial branches and even accomplish self fertilization in separate culture. No comparable latent femaleness was observed in the male strains.
- 7. Since each strain originated from a single uninucleate zoöspore the bisexual potentiality of the females affords strong support to Hartmann's theory of Relative Sexuality.
- 8. Six possible types of sexuality are postulated for *Sapromyces Reinschii*, 1, pure male (MM), 2, male with latent femaleness (Mf), 3, neutral, strongly sexed (MF), 4, neutral, weakly sexed (mf), 5, female with latent maleness (mF), 6, pure female (FF). Of these possible types, only three, namely 1, (MM), 4, (mf) and 5, (mF), appear to be represented among the single spore strains investigated in this study.

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# AN UNDESCRIBED FUNGUS ON JAPANESE CHERRY

E. S. LUTTRELL <sup>1</sup>
(WITH 10 FIGURES)

#### INTRODUCTION

For the past several years Japanese cherry trees, *Prunus serrulata* Lindl., planted as ornamentals on the Duke University campus have been observed to be infected by a fungus which produces tiny, black pustules upon the surface of young twigs. Attempts at classification of the fungus and a comparison with descriptions of species reported as occurring on members of the genus *Prunus* indicate that it has not been previously described. An investigation of its morphology and development, the results of which are contained in the following account was, therefore, undertaken.

# DEVELOPMENT OF THE FUNGUS

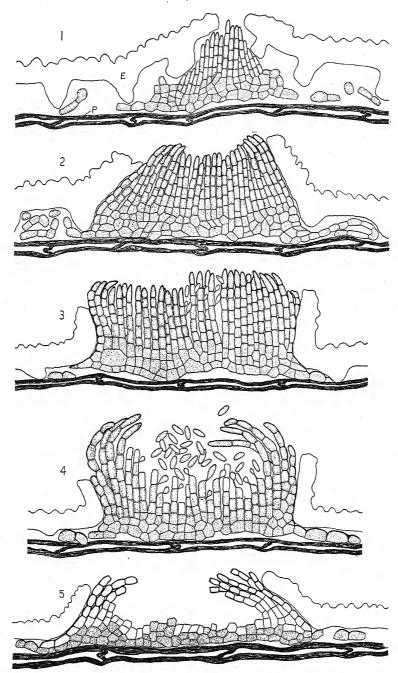
The first evidence of infection may be noted toward the end of July when black specks appear on the twigs of the current season's growth. By means of free-hand sections cut parallel to the surface, the specks are found to consist of small clusters of erect hyphae arising on the interior of certain epidermal cells. Adjacent cells contain irregular, branched mycelium which may coil and nearly fill the cell cavities. In vertical sections the mycelium is seen to be restricted entirely to the epidermis, this layer having been isolated from the subjacent tissues by periderm initiated during the preceding May. The activity of the fungus has resulted in a dissolution of the portions of the epidermal walls which lie toward the center of the stem, separating the epidermis from the underlying periderm. The mycelium now rests upon the periderm and is covered by the partially disintegrated epidermal cells and

<sup>&</sup>lt;sup>1</sup>I thank Dr. Frederick A. Wolf, Duke University, Botany Department, for his advice and criticism of the work and for his material assistance in the preparation of the manuscript.

the cuticle (FIGS. 1–5). Within the lumina of some of the cells, the hyphae have become compacted into a flat, pseudoparenchymatous stroma composed of large, irregularly polygonal cells from which arise erect hyphae (FIG. 1). The hyphae are unbranched and are divided into short cylindrical cells. This structure is the young acervulus and the erect hyphae are conidiophores in an early stage of development. The tips of the conidiophores are directed against the outer epidermal wall which has been raised and is beginning to rupture in consequence of the pressure developed by their elongation. The extreme tips of the conidiophores are becoming brown and thick-walled, but the rest of the acervulus and the mycelium remain hyaline. Each cell of the mycelium and of the acervulus is filled with a dense cytoplasm and possesses a single prominent nucleus located near the center of the cell.

As the season advances, the acervuli become more prominent though by late fall they hardly exceed  $100 \mu$  in diameter. Under the hand lens they appear as black, cushion-like protuberances, flat or even slightly concave above. The acervulus by this time has enlarged to occupy the space covered by several epidermal cells. By its growth in diameter the ruptured walls and cuticle have been pushed back centrifugally to form a collar surrounding the base of the acervulus (FIGS. 2, 6). A layer of hyphae similar in structure and origin to the conidiophores but distinguished from them by their thickened walls and brown color borders the acervulus. They are sometimes longer than the conidiophores and their tips may fold inward to some extent. These hyphae never produce conidia but seem to function only as protective hyphae. The browning and thickening of the walls of the tips of the conidiophores and of the protective hyphae probably result from their exposure to desiccation. A similar response may also be observed in the mycelial cells whose outer walls become thickened and darkened, giving a pale brown color to the entire mycelium.

The earliest stages in the formation of conidia are found during late March. This process involves first the distal portions of those conidiophores located toward the center of the acervulus (Fig. 3). The conidia arise laterally. In their formation, each cell of the conidiophore produces a sterigma at whose tip is borne a globular swelling (Fig. 7). At the same time, there is a division of the



Figs. 1-5.

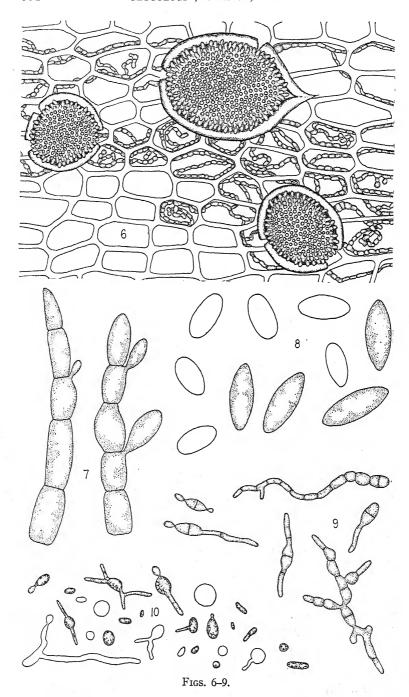
nucleus of the conidiophoral cell, one daughter nucleus remaining within the cell while the other migrates into the developing conidium, which is subsequently abstricted into the space between the conidiophores. While each cell probably repeats this process to form several conidia, it eventually becomes exhausted and disintegrates. As the distal cells are exhausted, other cells beneath them bear conidia and disintegrate in turn. The conidiophores, thus, gradually become shorter as the zone of conidial formation progresses towards the base of the acervulus (FIG. 4). As a result of the basipetal disintegration of the conidiophores, the protective hyphae bend inward and partially close the acervulus which is now filled with conidia (FIG. 4). An acervulus sectioned in this stage of development may resemble a pycnidium, and, upon superficial examination without knowledge of its development, the fungus might be mistaken for a pycnidial form.

After the conidia have been shed, the stroma and the basal portions of the peripheral protective hyphae remain as a shallow, crater-like receptacle. The rim of the receptacle gradually becomes blackened and broken, although the cells in the base of the stroma apparently contain living protoplasts until fall (Fig. 5). Further development has not, however, been observed. Disintegrating stromata may still be found within the epidermis which is being sloughed off from three year old twigs.

#### GROWTH IN CULTURE

Both mature and immature conidia may be obtained from the acervuli. Mature conidia are unicellular, elliptical and pale brown in color, while the immature ones are hyaline and shorter (FIG. 8). Both germinate readily either in drops of water or upon agar by the production of buds or one or more germ tubes (FIG. 9). They generally become transversely septate before germ tubes are formed.

The fungus was isolated by suspending from the top of a petri dish pieces of twigs bearing acervuli which were shedding conidia, thus making it possible for the conidia to fall upon the agar. The course of germination was followed by inverting the petri dish upon the stage of the microscope and observing the growth through the bottom of the dish. Within a few days, a powdery, white



layer developed over the surface of the agar. This layer soon thickened and became wrinkled to form pale-pink yeast-like colonies. Essentially similar colonies are produced on malt agar, on agar containing shredded cherry bark, and on synthetic agar. They are composed of masses of individual cells ranging in size from 7–25  $\mu$  in diameter, and in shape from spherical to oblong or elliptical (FIG. 10). Multiplication of cells results from budding although any cell may produce one or several germ tubes from any part of its surface. The tubes rarely reach a length exceeding 100  $\mu$ , and no septations are formed. They vary in diameter from 3–8  $\mu$ , and their diameter bears little relation to the size of the cell which produced them. Living cells are filled with coarsely granular, reticulated protoplasm. Many of the cells, however, are dead, appearing as empty hyaline elements.

#### TAXONOMY

The fact that the fruiting body is an acervulus composed of a basal, pseudoparenchymatous stroma bearing conidiophores over its upper surface and is erumpent from the epidermal cells places the fungus at once in the Melanconiaceae. Here, because of its unicellular, elliptical, sub-hyaline conidia, it belongs in the Hyalosporae among the genera *Gloeosporium*, *Myxosporium*, *Protocoronis*, etc. From these genera, however, it differs in several important respects: (1) The conidia are produced singly on sterigmata near the apex of each cell of the simple, multicellular conidiophore. Conidial formation is initiated on the apical portion of the conidiophore and progresses toward the base. It is accompanied by a dissolution of the exhausted cells. (2) The conidiophores are surrounded by a layer of thick-walled protective hyphae which arise along the periphery of the stroma.

A new genus distinguished by the above characteristics is, accordingly, erected in the Melanconiaceae. It is named *Catenophora* in recognition of the fact that the conidiophore is composed of a series of cells each of which may produce conidia.

# Catenophora gen. nov. (Etym. catena, chain; phora, bearer)

Acervulis innatis denique erumpentibus; conidiophoris simplicibus, a cellulis conidiferis constituentibus quae in catena disposuerunt atque quae seriatim ad basam dissiluerunt; conidiis continuis, ellipticis, conidiophorarum a lateribus orientibus, primo hyalinis, maturitate pallide-bruneolis.

# Catenophora Pruni sp. nov.

Myceliis intra epidermidem; acervulis pulvinatis, atris, innato-erumpentibus,  $80\text{--}160\,\mu$  diam., e hyphis sterilibus atque fertilibus efformatis; hyphis sterilibus centrifugis, flexuosis; conidiophoris (hyphis fertilibus) erectis, septatis, simplicibus, e stromate tenui oriundis,  $40\times4.5\,\mu$ ; cellulis conidiferis in catenis dispositis; conidiis pleurogenis, continuis, ellipticis, primo hyalinis, maturitate pallido-bruneolis,  $7\text{--}13\times3\text{--}4.5\,\mu$ .

Hab. in ramis vivis Pruni serrulatae.

Type specimens have been deposited in the Farlow Herbarium, Harvard University, Cambridge, Mass., The Mycological Herbarium of the United States Department of Agriculture, Washington, D. C., and the Herbarium of the New York Botanical Garden, N. Y.

#### SUMMARY

The development of a previously undescribed Melanconiaceous fungus which infects the twigs of Japanese cherry, *Prunus serrulata* Lindl., in the vicinity of Durham, North Carolina, has been studied. The fungus was found to be distinct from other members of the Hyalosporae section of the Melanconiaceae because of its method of formation of conidia. These are borne pleurogenously on simple, multicellular conidiophores. Conidial formation involves successively the cells from apex to base of the conidiophore. The exhausted cells disintegrate. The fungus has been named *Catenophora Pruni*.

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#### EXPLANATION OF FIGURES

Fig. 1, section of a young acervulus of Catenophora Pruni in late July at the time of rupture of the epidermal wall (note the mycelium lying between the periderm (p) and the partially disintegrated epidermis (e)); 2, section of a similar stroma in November; 3, an acervulus sectioned in late March in which conidial formation has been initiated on the distal portions of the conidiophores in the center; 4, an older acervulus (May) in which the apical portions of the conidiophores have become exhausted and disintegrated leaving a conidium-filled locule partially closed by the peripheral hyphae; 5, an exhausted acervulus; 6, surface view of acervuli and mycelium of C. Pruni within the epidermal cells in November; 7, conidiophores; 8, conidia—the fully mature conidia have been stippled; 9, germinating conidia; 10, cells from culture.

# AN ENTOMOGENOUS FUNGUS ON SPIDER MITES ON WATER HYACINTH

#### VERA K. CHARLES

While in Florida during the winter of 1938–1939, the author observed the frequent occurrence of spider mites, *Paratetranychus yothersi* (McGregor) <sup>1</sup> on the common water hyacinth, *Piaropus crassipes* (Mart.) Britton. Thinking that an entomogenous fungus might occur on these mites numerous plants attacked by them were carefully examined and as a result a fungus was found which though quite localized was evidently acting as a control. Its entomogenous character was evident from the fact that it was confined to the mites and did not spread over the surface of the leaves or in any instance penetrate the tissue of the host plant. In the natural condition it was observed that the mites were enmeshed in a fine web of white mycelium in which many individuals were dead.

The parasitism of the fungus was demonstrated by placing leaves infested by active, vigorous mites in paper bags under which condition the fungus grew rapidly on both the exterior and interior of the mites with the result that within 18 hours all the mites were dead.

#### DISCUSSION OF THE FUNGUS

A study of the fungus indicates that it may be considered a species of *Rhinotrichum*, a genus established by Corda (1) in 1837 and characterized by denticulate, sporiferous conidiophores and one-celled spores. Species of *Rhinotrichum* have generally been considered saprophytic though several parasitic species have been reported including two by Spegazzini, namely, *R. canescens* on *Cercospora sphaeroidea* on *Cassia occidentalis*, and *R. gossypinum* on *Cercospora Caricae* Speg. (*Asperisporium Caricae* [Speg.] Maubl.) on leaves of *Carica Papaya*. Still another species, *R. griseum* Sacc. was described on sori of *Phragmidium Rubi* (Pers.) Wint.

<sup>&</sup>lt;sup>1</sup> Thanks are due Dr. H. E. Ewing for the determination of the host.

It is appreciated that the form genus *Rhinotrichum* is badly in need of revision, and that certain species now assigned to it possibly including the entomogenous species should be transferred to other genera. The suggestion has been made that it represents the conidial stage of certain basidiomycetous fungi. However, further work will have to be done to demonstrate this relationship.

In the original diagnosis of the genus *Rhinotrichum*, Corda describes the conidia as simple, but does not mention their shape, although he does in that of his type species, *Rhinotrichum simplex*.<sup>2</sup> Saccardo (6, p. 91) in the emended diagnosis of the genus describes the conidia as ovoid or oblong, hyaline, pallid or bright colored. In most of the species of *Rhinotrichum* the conidia conform to this type, but in a few species they are described as globose or subglobose.

In the majority of the species the conidia are relatively large, frequently measuring  $14-15 \times 22-25 \mu$  or more and only a few species are described with conidia as small or smaller than  $5 \times 8 \mu$ . Of those having smaller conidia are two entomogenous species from Ceylon described by Petch, R. parvisporum and R. album (3, pp. 258-9). R. parvisporum (5, pp. 243-244) was reported by Petch as occurring on scale insects of the genera Aspidiotus and Lecanium. Discussing this species he remarks that it was found in a collection of leaves of Hevea in which some of the Aspidiotus were attacked by Pseudomicrocera and some of the Lecanium by Aschersonia marginata. However, R. parvisporum was not found on scales which bore these other two fungi. The fungus was described as forming a white fringe around the scale, and spreading over it in a loose weft. This species also occurred on an effete Gibellula on a spider. The possible parasitism of these two entomogenous species was not discussed, but in the case of R. parvisporum the mycelium encircled and spread over the scales.

R. parvisporum differs from the species on mites in several respects, such as the shorter, non-septate character of the conidiophores, their regular inflation (up to  $2 \mu$ ) and the smaller conidia.

<sup>&</sup>lt;sup>2</sup> This species has never been available for study and comparison, and therefore has not been accepted as the type species. (See The Genera of Fungi (Clements and Shear), p. 389. 1931).

In culture, according to Petch, this species frequently produces conidiophores in groups on the mycelium so that the fungus might be taken for a *Cladobotryum* with decumbent conidiophores.

The second entomogenous species, Rhinotrichum album, was described by Petch (3) in 1926 on Lecanium hemisphaericum. 1931 (4, p. 61) he stated that it was synonymous with Gonatorrhodiella coccorum described by him in 1925 (2, pp. 178-181). discussing this fungus Petch questioned its proper allocation to the genus Gonatorrhodiella calling attention to the manner of growth as follows: "The growth of the conidiophores is definite. It terminates in a definite, apical segment and does not subsequently grow through that segment," adding that "the apical segment is formed before the swellings on the conidiophore." In reference to the synonymy of R. album and G. coccorum (4, p. 61) Petch stated that "further collections of this fungus (R. album) and their culture on Quaker Oat agar have shown that it is the same as G. coccorum Petch." While the synonymy of these two species is announced there is no formal combination of the name or an emended or additional description of the fungus. The original descriptions of the two species G. coccorum and R. album differ in several characters. In G. coccorum the conidiophores are 0.2 mm. high, in R. album 0.1 mm., in G. coccorum they are described as inflated below each septum, while in R. album they are described as equal and slightly broader and clavate at the apex.

In the early description of *G. coccorum* mention is made of a whorled arrangement of the sterigmata below the septa as well as a scattered arrangement over the terminal segment and along the conidiophore. In addition the conidia are in chains, a character not mentioned in the description of *R. album* or of any other species of *Rhinotrichum*. A slight difference is also noticed in the size of the conidia in the respective descriptions of these two species. It is quite possible that these differences may be due to the age and condition of the material. However, in view of these discrepancies and in the absence of an emended description, the lack of material for comparison, and the occurrence of the fungus on an unrelated host the writer hesitates to allocate the fungus on mites to *R. album*. Therefore it is thought best to describe the

fungus on the mites as new even though later it may be shown to be Petch's species. Accordingly, the fungus is designated R. depauperatum and described as follows:

## Rhinotrichum depauperatum sp. nov.

Effuse, cobwebby, white to pale gray in age; sterile hyphae repent or suberect; fertile hyphae long, 75–200  $\mu$  or longer, 1.5–2  $\mu$  in diam., ascending, flexuous, closely septate, sometimes slightly enlarged below the septum, terminal cell ovate-conoid and sporiferous; conidia borne on sterigmata along entire length of the conidiophore, sterigmata 1–2  $\mu$  in length, conidia ovoid, 1.5–2  $\times$  2.5–3  $\mu$ , smooth, hyaline.

Late effusum arachnoideum, albo-griseum; hyphis sterilibus repentibus vel ascendentibus; hyphis fertilibus perlongis, 75–200  $\mu$  vel longioribus, 1.5–2  $\mu$  diam., ascendentibus, flexuosis, breve septatis, interdum infra septa leniter inflatis, cellula terminali ovoideo-conoidea et sporigena; conidiis in sterigmatibus 1–2  $\mu$  longis per longitudinem totam conidiophori, ovoideis, 1.5–2  $\times$  2.5–3  $\mu$ , levibus, hyalinis.

On Paratetranychus yothersi (McGregor) on leaves of Piaropus crassipes (Mart.) Britton. Type collected at Maitland, Florida, Jan. 1939 and deposited in the Mycological Collections of the Bureau of Plant Industry (No. 72565). A portion of the type collection deposited in the herbarium of the Florida Agr. Exp. Sta., Gainesville.

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## MYCOLOGICAL NOTES. IV

C. L. SHEAR

## 16. SPHAERONAEMA Fries

Various interpretations of the characters and limitations of this genus have been made since it was first described by Fries as Sphaeronema Obs. Myc. 1: 187. 1815. The question may be raised as to whether the name should be spelled Sphaeronema as Fries originally used it or Sphaeronaema as changed by him in Syst. Myc. 2: 535. 1823, and Summa Veg. Scand. 400. 1849. The change was made, he says, because the Greek nema means thread and does not seem as appropriate as naema referring to the out-flowing of the spore globule. Saccardo and recent authors follow the later form. Sprengel likewise considering nema inappropriate also suggested a new name for the genus, Sphaeromyxa in Linn. Syst. Veg. Ed. 16, 4: 406. 1827, and transferred all of Fries' species. Fries described the genus Sphaeronema as having "perithecia" of various shapes, frequently stalk-like or cylindrical with spores forming a gelatinous globule at the apex. Ten species, most of which had previously been referred to Sphaeria, were included and two were illustrated, S. cladonisca Obs. Myc. pl. 2, f. 7 showing various forms, and S. ventricosa l.c., pl. 2, f. 8. Fries again in Syst. Myc. 2: 535. 1823, described it in the same way and included 15 species, the first being S. subulatum. His next treatment was in Summa Veg. Scand. 400. There he lists 12 species, dividing them into three subgenera on the basis of the character of the pycnidial wall. Zythinia. Pycnidia soft waxy, including S. subulatum, S. rufum and S. aciculare. (b) Melanocybe. Pycnidia carbonaceous and spore globule black. (c) Genuina. Pycnidia horny carbonaceous and spore globule white. The first species in the last group, which from the name he evidently intended to be regarded as typical, is S. cladoniscum, the second S. cylindricum. In the meantime Corda Icon. Fung. 1: 25. 1837; 3: 27. 1840; 4: 39. 1840; and 5: 31. 1842 had used the name and added several new species. The first species he described was *S. vitreum* 1.c. 1: *f.* 297. He modified Fries' description somewhat, restricting its application to forms with membranaceous or coriaceous-fleshy pycnidia with more or less elongate necks and simple spores. Corda appears to have been the first to give a description and illustration of spores of the genus. He also says very emphatically "asci nulli!"

During the period between Corda and Saccardo very little was added to the knowledge of this group. Until the introduction of the type method of fixing, in part at least, the application of generic and specific names only general macroscopic characters were used in separating these groups. As microscopic characters were studied and described, greater importance was placed on the character of the tissues of pycnidial walls, and the spores and sporophores. Saccardo Syll. Fung. 3: 185. 1884, accepted the genus as originally described by Fries, except that he restricted it to species having hyaline or sub-hyaline, simple spores and included 83 species. In 1896 Jaczewski published a monograph of the genus, Monographie du genre Sphaeronema Fries. His concept was similar to that of Saccardo, but much broader. He did not designate a type, but after discussing the various descriptions of Fries, Montagne, Karsten and Saccardo, gave a revised description which translated is as follows:

"Pycnidia membranaceous, coriaceous or soft fleshy, black carbonaceous or colored, innate or superficial, cylindrical, pyriform, or globose with emerged beak or ostioles, spores hyaline or subhyaline, rarely brown, simple or plurilocular." He included 72 species which, according to some recent authors, includes members of various widely separated genera.

Von Höhnel in 1917, Hedwigia 59: 273, undertook a revision of this genus, fixing its application by the type method. He selected as type the first species in Fries' list in Syst. Myc. 2: 535. 1823, which was S. subulatum (Tode) Fries. Having chosen this species it was necessary to determine exactly what plant this name really belonged to. This problem was not so easy to solve. Tode, Fungi Meckl. 2: 44. pl. 15, f. 117. 1791, described and illustrated Sphaeria subulata, but just what Tode had can not be determined

with certainty at present, as none of his specimens are extant, and his description might apply to either a pycnidial or a perithecial form. From his statement that the spore globule which forms at the ostiole becomes black, it appears that he probably had a Melanospora and not one of the group of fungi to which the name Sphaeronaema has been applied by Fries and later authors. The question then arises what was the plant to which Fries applied the name subulata? This species is No. 6 in his first list, Obs. Myc. 1.c., without description. He cites Sphaeria subulata Pers. and also Tode as synonyms. In Syst. Myc. 1.c., he cites Tode and Persoon and Albertini and Schweinitz, also Nees, Syst. Myc. f. 345, but most important of all for purposes of exact identification is his citation of his own Scleromyceti Sueciae 325. The specimens of this number which we have examined were unfortunately destroyed by insects or show no fructifications of a Sphaeronaema. Von Höhnel, Frag. Myc. 32, 1902, says he did not see Fries' specimen of this species and bases his identification of it on a specimen of Fuckel, Fungi Rhen. 773, which was described by Fuckel as the type of a new genus of ascomycete, Eleutheromyces. Notwithstanding the fact that Fuckel described, illustrated and gave measurements of the asci, von Höhnel maintains that Fuckel's fungus is a pycnidial form identical with that described by Fries as S. subulata and that therefore Sphaeronaema Fries and Eleutheromyces of Fuckel are synonyms. This seems entirely unjustifiable. Unfortunately von Höhnel's statement was accepted in Clements and Shear, The Key to the Genera of Fungi 360, where Eleutheromyces as a synonym should be deleted and the type of Sphaeronaema changed to S. cylindricum. The question of the real nature of Eleutheromyces will be discussed later. Fortunately, Petrak and Sydow were able to examine a good original specimen of Sphaeronaema subulatum Fries from Fries' Herbarium which they describe, Ann. Myc. 21: 361. 1923, as follows: Fructifications on the upper surface of the pileus and gills of an agaric, scattered, superficial, very variable in form, globular or oval, more or less elongated into a beak with round apex, 200-400 μ in diameter, wall of several layers of irregularly rounded hyaline cells; conidiophores covering the whole inner surface of the wall; neck filiform and very variable in length, simple or somewhat branched scarcely a micron thick; conidia united in a slimy mass, elongate elliptical, 1-celled, somewhat inequilateral with an indistinct hyaline cilium about  $6 \times 0.5 \,\mu$  at the apex. At the base of the spore there is a portion of the sporophore attached about 1.5-2.5 µ long. This is the fungus which Grove (British Stem & Leaf Fungi 2: 115. 1937.) describes and figures as Sphaeronemella subulata comb. nov., and A. L. Smith (Trans. Brit. Myc. Soc. 1: 199. 1897.) as Sphaeronemella oxyspora (Berk.) Sacc. The fungus which von Höhnel found on one of Fuckel's specimens (No. 773) is probably the same, but is not the fungus which Fuckel described and illustrated as *Eleutheromyces*. If Sphaeronaema subulatum Fries be accepted as the type of the genus, as von Höhnel maintains, it would restrict the application of the name to a very small group of species of the Nectrioidaceae and change almost entirely the current usage of the name as applied by Saccardo and recent authors.

Petrak and Sydow l.c., in discussing Sphaeronaema, maintain with much more reason that S. cladoniscum or S. cylindricum which are the first two species mentioned and illustrated by Fries, Obs. Myc. l.c., and are also the first species under Fries' section Genuina in Summa Veg. Scand. 400. 1849, should be taken as the type. These two names are regarded as synonyms by von Höhnel and recent authors. This would make Sphaeronemina von Höhnel, l.c. p. 274, a synonym of Sphaeronaema, both having the same type, S. cylindricum (Tode) Fries.

More information regarding the taxonomic value of the various criteria which have been used in segregating genera in this group and also regarding their life cycles must be obtained before any great improvement can be made in their classification. Von Höhnel states that a dozen or more genera are represented by the species included by Saccardo. Some of these new genera which he has proposed, however, are of doubtful value.

# 17. SPHAERONAEMELLA Karst.

This genus was described in Hedwigia 33: 17. 1884, with the monotype S. Helvellae Karst., specimens of which were distributed

by the author in his Fungi Fenniae Exsiccati as no. 674. Jaczewski in his monograph of Sphaeronema, p. 303, 1896, states that he examined Karsten's type and that the pycnidia have long, cylindrical, spirally twisted, penicillate beaks and spores  $9 \times 4.5 \mu$ . No sporophores are mentioned. Later Diedicke, Krypt.-Fl. Brand. IX. 4: 694. 1914, states that the original specimen of Karsten's fungus which he examined showed the pycnidium to be parenchymatic and the beak composed of long fascicled hyphae, sporophores lacking, spores simple, elliptical  $7-13 \times 4-6 \mu$ . Von Höhnel discusses this genus in Hedwigia 60: 151-155. 1918, and states that he had not seen the original specimens of Karsten's fungus, but that according to the accounts of Jaczewski and Diedicke as cited, since no sporophores were found, he has no doubt that Karsten's fungus is an ascomycete very similar to Ceratostomella in which the asci have disappeared, but belonging to the Hypocreaceae. For a fungus similar in appearance to Karsten's, but which he regards as a pycnidial form, he establishes a new genus, Hyalopycnis, with the type H. hyalina von Höhnel, and adds two other species, H. vitrea (Corda) von Höhnel and Sphaeronaema blepharistoma Berk., Mag. Zoöl. & Bot. 1: 512. 1837. He characterizes the genus as having superficial, transparent pycnidia provided with thick beaks with fimbriate ostioles, and branched sporophores with single, elongate-cylindrical, 1-celled, hyaline conidia  $6-14 \times 2.6-3.5 \mu$ . The character which he regards as most important and which he says separates the type from the species which are usually placed in Sphaeronaemella, is the plectenchymatic structure of the pycnidium, and the closely parallel, hyaline, thin-walled, sparingly septate hyphae in the beak. From the information thus far available and until much more evidence is produced, it does not seem that von Höhnel is justified in treating Karsten's fungus as an ascogenous genus, and therefore we consider his Hyalopycnis as a synonym of Sphaeronaemella Karst.

Grove, British Stem and Leaf Fungi 2: 115. 1937, has emended the description to include spores having appendages and has transferred *Sphaeronaema subulatum* Fries to *Sphaeronaemella*, making the new combination *S. subulata* (Fries) Grove and including *Sphaeronaema oxysporum* Berk. as a synonym. We are

inclined to accept this treatment of the genus until more satisfactory information is obtained in regard to the structure and life cycles of the species involved. If Grove's concept of this genus be accepted it follows as intimated in his note (l.c. p. 116) that Eleutheromycella von Höhnel, Frag. Myc. 178, 1908, becomes a synonym of Sphaeronaemella. The type of von Höhnel's genus, E. mycophila, apparently differs from Sphaeronaemella subulata (Fries) Grove in having a conical papilla instead of a beak on the pycnidium, and in longer spores and setae.

## 18. Eleutheromyces Fuckel

This genus was described by Fuckel, Symb. Myc. 183. pl. 4, f. 52. 1869. It was based on a single species which he called E. subulatus Fuckel. He cites Sphaeronaema subulatum (Tode) Fries, Syst. Myc. 2: 536, as a synonym and his own specimen No. 773 in Fungi Rhenani Exsiccati on a decaying agaric as representing the species. As already stated above under note 16, von Höhnel examined a specimen of this number, and finding only free spores concluded that Fuckel was mistaken in his description and did not have an ascomycete, in spite of the fact that he described and illustrated asci and ascospores and gave measurements of the asci  $(52 \times 2.5 \,\mu)$ . That there is an ascomycete on decaying agarics corresponding to Fuckel's description and illustration seems proven by the evidence of later mycologists. Winter (Die Pilze 2: 93. 1887.) reports the species on Polyporus betulinus and gives the following measurements: Asci  $48-52 \times 2.5-3 \mu$ , ascospores 4-6  $\times$  1.5  $\mu$ . His illustration, however, on page 84 is evidently copied from Fuckel.

Petch (Jour. Bot. 73: 186. 1935.) pointed out von Höhnel's error in assuming that Fuckel's fungus was not an ascomycete, and cited Sacc. Syll. Fung. 17: 779. 1905, and 22: 1142, 1913, where Saccardo states that there is an ascogenous fungus agreeing with Fuckel's description. Saccardo (Michelia 1: 50. 1879.) also describes a specimen which he collected in Italy in 1876 which had asci  $50 \times 4 \mu$  and ascospores  $5-6 \times 1.75-2.5 \mu$  with setae at each end. Saccardo also states that there is a pycnidial fungus very similar in appearance to *Eleutheromyces* which may be part of its life cycle. The best illustration of the ascogenous form of this

fungus is found in Ellis and Everhart, N. Am. Pyren. pl. 14, f. 6–12. 1892. It is possible, however, that this may represent a different, but closely related species, as the asci and ascospores do not agree well with Fuckel's illustration. From the evidence submitted above it seems rather conclusive that von Höhnel's statement that Fuckel's fungus is a pycnidial form which he regards as the Sphaeronaema subulatum of Fries and which he takes as the type of the genus Sphaeronaema is a mistake.

## 19. SPHAERIA PUGILLUS Schw.

This fungus was described by Schweinitz in his Syn. Fung. Car. 38. 1822, as follows:

107. Pugillus Sz.

S. circinata majuscula immersa atra, ostiolis in cylindrum compressum conflatis, supra divergentibus, singulis capitulo lutescente coronatis.

Ad ligna dura acerina cortice orbata crescens, non male refert pugillum clausum. Profunde in substantiam ligni immersae sphaerulae sunt circinantes aterrimae, numerosae, circumdatae materia alba, e ligno orta. Ostiola connata in cylindrum compressum, interdum oblongo-ellipticum ascendunt per lignum et ad semilinearam altitudinem supra lignum. Tum cylindrus dividitur in 3, 4, 5 ostiola divergentia, ut digiti pugilli subclausi. Horum singulum est forma cylindrica, transversim plicatum, aterrimum, coronatum capitulo, sphaeriae forma, lutescente, viridi pruinato, pupilla nigra.

Fries in Syst. Myc. 2: sec. 2, p. 383. 1823, also describes this species as follows:

135. S. Pugillus, ligno immersa, superne conceptaculo tecta, stromate albido, ostiolis in cylindrum compressum conflatis, supra divergentibus. Schwein.! l.c. n. 107.

Priori affinis, stromate subdisco lutescente. In ligno nidulant perithecia circinantia, numerosa (minus conferta, quam in priori) stromate ligneo cincta. Cylinder erumpens (conceptatulum) dividitur in ostiola 3–5 divergentia. "quorum singulum est forma cylindrica, transversim plicatum, aterrimum, coronatum capitulo, Sphaeriae forma, lutescente, viridipruinato, papilla nigra" Schwein. l.c. Ad ligna duriora acerina cortice orbata in Carolina. (v.s.)

Fries' description was evidently based on a part of the original specimen described by Schweinitz.

In 1832 Schweinitz in his Syn. N. Am. Fung. 200, No. 1322, lists the species as follows:

1322. 175. S. Pugillus, L. v. S., Syn. Car. 107, F. 135, in putrido ligno etiam Pennsylvania obvia, quanquam rara.

The next mention we find of this species is by Curtis, Geol. & Nat. Hist. Surv. N. Car. III, Bot., p. 142. 1867, where he lists it as *Valsa pugillus*. In 1878 W. C. Stevenson, Jr., published an article, entitled "Additions to Mr. Cooke's paper on the Valsei of the United States," Proc. Acad. Nat. Sci., Phil. 30: 86–88. 1878, in which he has the following note on a specimen of this species which he found at the Philadelphia Academy:

# "97. Valsa pugillus, Schw. Am. Bor. 1322. Evidently a Sphaeronema."

As noted by Schweinitz, Syn. N. Am. Fun. l.c., he had two specimens which he referred to this species, the original from Salem, North Carolina, and the other from Pennsylvania. The specimen referred to by Stevenson was probably that from Pennsylvania, which is found in the mounted collection of Schweinitz' fungi at the Philadelphia Academy. The next mention of it we find is by Cooke, Grevillea 13: 38. 1884. He refers this species to *Sphaeronema*, simply quoting Stevenson, l.c. Ellis and Everhart in N. Am. Pyren. No. 470, 1892, also cite Stevenson's note.

There is no evidence that either Cooke or Ellis examined an authentic specimen. As we have pointed out before, Schweinitz' habit of including specimens from Pennsylvania or other localities in the same packet with the original material from North Carolina has led to much confusion in the interpretation of his species and this probably accounts for the fact that Stevenson found a "Sphaeronema" in Schweinitz' specimen. We have not examined the specimen in the mounted collection.

Fortunately there is still preserved in Schweinitz' original autographed packet a small specimen which agrees perfectly with his original description as quoted above and also that given by Fries, which was evidently from part of the same specimen. It bears a portion of a gummed paper strip which indicates that it was from his early material which he had first mounted on sheets with gummed strips. There is also a bit of this same specimen in the Michener herbarium in the Bureau of Plant Industry Collections. We have made four gatherings of specimens which agree with this

species and from a study of these and the original specimen referred to we find they clearly belong to the genus Camarops, as we have interpreted and discussed it in our Mycological Notes II, Mycologia 30: 586. 1938. The stromata are entirely buried in the much decayed wood of old logs of deciduous trees. The ostioles are united in a more or less erumpent disk which, when fully developed, shows the characteristic appearance suggested by Schweinitz' specific name pugillus. The wood in which the perithecia are embedded is usually a pale yellowish or saffron color. The perithecia are crowded and membranaceous or somewhat coriaceous and subglobose to flask shaped, irregular and beaked. beaks vary greatly in length. In many cases they do not project above the surface of the stroma. The ascospores are pale yellowish, elliptical, 5-6  $\times$  2.4-3  $\mu$ . They have the thin hyaline envelope characteristic of the other species of this genus. It will be noted that the spores are almost identical in size, shape and general character with those of C. lutea (Alb. & Schw.) Shear and it is possible that this may be a variety of that species, though in the abundant material we have collected we have found no stromata which quite match the smallest in the material illustrated in our figure 1, l.c. We propose for Schweinitz' plant the name Camarops pugillus (Schw.) Shear comb. nov. Besides the type we have seen only the following specimens which we have gathered:

No. 5593, on decaying log of maple or *Liriodendron*, Arlington Cemetery, Va., Mar. 1927.

No. 4238 on beech log, Arlington Co., Va., Oct. 22, 1933.

No. 4237 on Liriodendron, Arlington Cemetery, Va., Feb. 1939.

No. 4239 on Rhododendron, Indian Gap, Tenn., Aug. 1939.

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# STUDIES ON CARYOSPORA PUTAMINUM 1

WALTER F. JEFFERS

(WITH 2 FIGURES)

#### INTRODUCTION

Caryospora putaminum is an Ascomycete belonging to the family Sphaeriaceae. It is of world-wide occurrence, having been reported in North and Central America, China, France, Germany, India, Italy, and Japan. This organism appears to be strictly saprophytic, occurring mainly on old peach stones. It has also been found on acorns, hickory nuts, seeds of "Buckaniana latifolia," Prunus cerasus, and Prunus domestica, and on old wood of Maclura aurantiaca. The author has collected it recently at Berwyn, Md., on a piece of coconut (Cocos nucifera) shell.

Caryospora putaminum has been described many times, but with the exception of the gross description of perithecia, asci, and ascospores, no detailed study has been made. As this fungus has large perithecia and ascospores, it was considered a good subject for cytological, anatomical, and cultural studies.

During these studies on *C. putaminum* another form of this genus was found which differed from all previously described species. A complete description of this form is given, and it is described as a new species.

#### CULTURAL STUDIES

In order to determine the best conditions for perithecial production, various culture media were tested under different environmental conditions. Best growth occurred on peach-stone extract agar and on pea-extract agar. Good growth also occurred on regular malt-extract agar. The peach-stone agar was made by boiling peach stones containing perithecia of *Caryospora putaminum* and adding this extract to the ingredients of malt-extract agar.

<sup>&</sup>lt;sup>1</sup> Scientific Contribution No. 501, Department of Botany, University of Maryland Agricultural Experiment Station.

The pea agar was made by adding the juice from fresh or canned peas to malt-extract agar.

On peach-stone agar young cultures were olive-grey in color; as they matured the aerial mycelium generally turned dark brown, while the substrate became black. When cultures were grown on rather concentrated pea extract agar, juice from 400 gms. of fresh peas per liter of agar, the mycelium varied from light grey to white in color. The aerial mycelium formed a dense layer, which became very wrinkled and sometimes cracked. Perithecia did not occur on this medium, but spermagonia and sclerotia were sometimes produced. When the pea extract was about half as concentrated as above or when juice from canned peas was used, the mycelium was light brown in color, and most cultures produced spermagonia in abundance. Perithecia occasionally formed on this less concentrated medium.

On peach-stone agar perithecia were produced over a pH range of 4.7 to 6.7; best production occurred between 5.0 and 6.0. On pea-extract agar spermagonia were produced over a pH range of 4.2 to 6.5; best production occurred between 4.7 and 6.0. The maximum and minimum pH values at which perithecia and spermagonia were produced varied somewhat in different isolants.

The optimum temperature range for growth of *Caryospora putaminum* is about 25–28° C. The maximum growth limit is close to 35° C., while the minimum temperature at which growth will occur is below 5° C.

Good growth and production of perithecia occurred when cultures were stored in semi or total darkness; but when cultures were placed in full sunlight, growth was somewhat decreased and only a few perithecia were formed.

Attempts were made to determine if there were any differences in cultures from 2, 3, and 4-spored asci. In one experiment whole asci containing these different numbers of spores were isolated, and in another test single spore isolations were made of each spore from 2, 3, 4, and 5-spored asci. In each instance there was no difference in the type of growth, and all of the resulting perithecia contained asci with various numbers of spores; as usual, 3-spored asci predominated.

#### ANATOMICAL AND CYTOLOGICAL STUDIES

Perithecia: Typical perithecia are 0.5-1.2 mm. in diameter and usually about the same in height. They are black in color and carbonaceous in texture. Naturally produced perithecia are usually slightly longer than broad, but in culture this ratio may be reversed. Mature perithecia are conical in shape and converge abruptly to a narrow tip containing a circular ostiole. The ostiole is about 0.1 mm. in diameter. The perithecial wall is usually about 125  $\mu$  thick, being composed of thick-walled cells which make up definite pseudoparenchymatous tissue. These cells are roughly rectangular in shape, average about  $8 \times 6 \mu$ , and are uninucleate. Perithecia which occur on peach stones have no basal parenchyma, the sides being attached directly to the substrate. This may also be true of perithecia in culture, or the wall may completely enclose the perithecial contents. On peach stones the perithecia are entirely superficial, but in culture they may be partly sunken. A peach pit containing perithecia of Caryospora putaminum is shown in figure 1. A.

Perithecia occur both inside and outside intact peach stones. Sometimes so many perithecia are inside that the entire cavity becomes filled with a mass of ascospores. At other times perithecia are only on the inside, and sometimes only on the outside of the stone. Pits which are so firm that they must be forcibly opened often contain perithecia. Their origin is possibly due to mycelial strands which enter small openings at the union of the two halves of the stone or which travel through the canaliculi of the stone. Small compact perithecia have been found within these canals.

Nearly mature perithecia contain a dense mass of paraphyses and asci. Apparently there is a gelatinous secretion present, for the perithecial content is jellylike and expands and contracts according to the moisture conditions. When mature perithecia become moist, the contents swell and ascospores are exuded through the ostiole as a sticky mass.

Collections of perithecia were made during each month of the year to study the seasonal development of asci and ascospores. Asci and spores in different stages of development were always

found. In natural material most spores mature during warm weather, spore discharge taking place during wet periods. Isolations have frequently been made from spores collected during the winter months; and as these spores gave good germination, it appears that this is the main method of overwintering. Ascospores are able to withstand periods of dryness, for stones kept in the laboratory for 2 months still contained spores which gave 100 per cent germination.

In culture the first definite evidence of a perithecium is a small knot of hyphae about 20–40  $\mu$  in diameter. Soon an outer wall of pseudoparenchymatous tissue becomes evident. This wall surrounds a mass of thin-walled, densely cytoplasmic cells which appear to be uninucleate. When the perithecium is about  $1\frac{1}{2}$  months old, larger cells become visible in the center of the perithecium. These cells appear to be the primary ascogenous hyphae, for soon a fertile layer develops in the base of the perithecium. From this layer of ascogenous hyphae the young asci arise and grow up through the thick mass of paraphyses which had previously formed.

Asci and ascospores: Caryospora putaminum has not been observed to produce eight-spored asci. The most frequent number of spores per ascus is three; next in abundance are 4, 2, 5, 1, 6, and 7 in the order listed. These figures hold true for artificially and naturally produced material. Table I summarizes the occurrence of asci containing various numbers of spores in naturally and artificially produced perithecia.

TABLE I

Occurrence of Asci Containing Various Numbers of Spores in Naturally and Artificially Produced Perithecia

Number of spores	Asci produced
per ascus	Naturally Artificially
1	
2	
3	222 180
4	153 86
5	4
6	6 1
7	2
8	0 0

Asci of this organism are large, some attaining a length of 300  $\mu$ 

and a width of 75  $\mu$ . The ascus wall is very thin and evanescent, usually being rather difficult to see. The ascus is club-shaped, rounded at the top, and tapers to a rather slender stalk at the base. Asci and ascospores are shown in figure 1, B and C.

Asci originate either from normal crozier development or as a swelling of a branch of the ascogenous hyphae without crozier formation. The ascogenous hyphae are so branched that they are very difficult to follow in sectioned material. Smear mounts show that the branching is irregular and very profuse.

Normal croziers have been observed in which fusion had just occurred in the penultimate cell while the ultimate and antipenultimate cells, each containing one nucleus, were about to fuse. Fusion nuclei vary from 3.5 to 6.0 µ while accompanying nucleoli range from 1.5 to 2.6 µ. Asci remain in the uninucleate condition until they are quite large. The general size of asci containing the fusion nucleus is  $34 \times 9 \mu$  to  $85 \times 20 \mu$ . This is by far the commonest stage in ascus development to be observed. As the fusion nucleus prepares to divide, the nucleolus disappears and a number of small, round chromatin bodies become evident. These ball-like particles are connected to one another by a network of chromatic strands. Usually there are ten or more such particles per nucleus. Other stages in the division of the fusion nucleus were observed, but no chromosome counts were obtained. To determine the possibility of a daily periodicity in the nuclear divisions in the asci, material was fixed at various times during the day and night. Only a few nuclear divisions were observed in any of this material. A few binucleate asci were noted and in one instance a young 3-spored ascus was found which contained one nucleus per spore while five nuclei remained in the epiplasm. Frequently asci were noted with nuclei in the epiplasm; the spores of such asci contained one nucleus in each of their two main cells. It seems likely that each spore contains one nucleus which divides to form a binucleate spore. This was found to be true in a young 3-spored ascus where the median spore septations had not yet formed; here there was one nucleus in each spore and two of these nuclei appeared to be in an early stage of division. Soon after the spores become binucleate a median septum is formed so that each cell contains one nucleus. Each ascospore is surrounded by a distinct hyaline envelope.

Asci containing one or more abortive spores have been noted. Nuclei could not be seen in such spores. Nuclei which are not originally included in a spore are left in the epiplasm and finally disintegrate.

Ascospores are delimited, as usual in the Ascomycetes, by the process of free cell formation. Young asci contain much dense cytoplasm but before spores are delimited they become quite vacuolate. Soon the outer spore walls and the median septum appear; these are followed by the terminal septations. Each spore contains one distinct median septum and from one to seven septa in each of the narrow tips. Only the two main cells contain nuclei. These nuclei average about 3.3  $\mu$  in diameter while the nucleoli average about 1.5  $\mu$ . The spores at this time are hyaline but soon a brown pigment begins to appear in the form of circular spots over the external walls. These spots merge and finally the mature ascospores are solid black in color. Mature spores are brittle in texture.

Measurements of several hundred ascospores showed an average size of  $97 \times 45 \,\mu$ . The largest spore so far noted was  $139.1 \times 65.6 \,\mu$ . As the number of spores per ascus increased, the spore size decreased; this is shown in the following measurements:

Spores from	Average size of spore, u
2-spored asci	

Most spores were slightly more than twice as long as wide. Occasionally spores occurred which were very abnormal in shape, some being very slender while others were almost spherical.

Ascospores germinate in two to three days when placed on a favorable medium. Two germ tubes are produced, one from each tip. Often the hyaline envelope which surrounds each spore prevents the immediate exit of the germ tube. In such instances the tube bends back and grows between the spore wall and the envelope. Many branches arise, and finally the envelope is ruptured in such a manner that the spore appears to have many germ pores. Germ tubes are  $4-6\,\mu$  in diameter at the base and taper to  $1-2\,\mu$  at the tip. Many branches are formed, and soon each spore is

surrounded by radiating strands of mycelium. Many anastomoses of various types occur in the young mycelium. Most mycelium is uninucleate, but multinucleate hyphae also occur.

The aerial mycelium of Caryospora putaminum is brown in color, sparsely septate, and varies from 1.0 to  $3.8\,\mu$  in diameter. Old hyphae possess knoblike thickenings over the outer surface. These thickenings form gradually, and various stages in their formation are usually noticeable. Nutritive mycelium lacks the wall thickenings and usually is more irregular in size. The usual diameter is from 1.5 to  $5.0\,\mu$ , but swellings frequently occur which attain a diameter of  $15\,\mu$ .

Paraphyses are very long and slender, some being  $500~\mu$  in length; their width varies from 1 to  $3.5~\mu$ . They are septate, each cell being uninucleate. Tips of paraphyses are pointed. A number of division figures have been seen in paraphyses, but due to their small size it was difficult to make any detailed study. The chromosomes appear to be spherical but lie so close together that they usually appear as a constricted rod-shaped body. At anaphase there are apparently two groups, each containing three or four of the spherical chromosomes.

Spermagonia and spermatia: When cultured on pea-extract agar, Caryospora putaminum forms small black carbonaceous spermagonia (FIG. 1, D). These are from 150 to 300  $\mu$  in height and from 120 to 180  $\mu$  wide. When mature, a circular ostiole about 30  $\mu$  in diameter is present in the top. The walls of the spermagonium are about 40  $\mu$  in thickness and composed of a pseudoparenchymatous tissue. Spermatia are exuded through the ostiole as a white cohering mass; they usually form a white ball-like body on the spermagonium.

The spermatia are produced from short sac-like stalks which line the interior of the spermagonium. Spermatia are single-celled, hyaline, and measure about  $2.8 \times 1.9~\mu$ . Examination of unstained spermatia shows one or two small circular bodies in each cell. These same bodies are evident when spermatia are stained in aceto-carmine. When fixed in chromo-acetic acid or Flemming's medium, the spermatia do not show these round central bodies but do show dark crescent-shaped bodies which usually lie against the wall. These curved bodies are evidently chromatic in nature but

do not have the appearance of the other nuclei observed in this organism.

Transfers from the masses of spermatia on the spermagonia gave normal cultures of *Caryospora*, but since it was possible that a strand of mycelium was also transferred, hanging-drop cultures of spermatia were made. Drops of various agars were placed on sterile cover slips, inoculated with spermatia and sealed to sterile depression slides. These slides were examined daily for 10 days, but no evidence of germination by the spermatia was noted. Conditions for growth were favorable, for strands of mycelium which were transferred at the same time made good growth.

Most evidence indicates that spermatia are not absolutely necessary for sexual reproduction of *Caryospora putaminum* and are not concerned in dissemination. Points in favor of this view are as follows:

- 1. Spermagonia and spermatia were not observed to occur in nature.
- 2. No cytological evidence of spermatia acting as fertilizing agents could be found.
- 3. Most cultures did not form spermagonia and perithecia on the same medium.
- 4. When spermagonia and perithecia occurred in the same culture, the spermatia were not discharged until the perithecia were nearly mature.
  - 5. Spermatia were not observed to germinate.

Apparently the initiators necessary for formation of perithecia and spermagonia are very similar, for cultures producing most perithecia on malt agars also form most spermagonia on peaextract agar. Also when spermagonia and perithecia do occur in the same culture, the two structures may fuse to form a compound fruiting body. Spermagonia have been noted to occur as sunken cavities in the upper part of perithecia.

Sclerotia: Occasionally, on pea-extract agar, small white structures arose directly from the agar surface. These masses were irregular in shape; some were spherical, while others formed a thin layer. Upon examination, this material was found to consist of irregular-shaped cells which formed a sclerotium-like tissue. Transfer of this tissue gave normal cultures of Caryospora. No

similar material was observed to occur in nature, and in culture it is of rare occurrence.

#### TAXONOMIC STUDIES

The differentiating characters used in the description of the various species of Caryospora were obtained from the following sources: Arnaud (1), Currey (2), Ellis and Everhart (3) and (4), Fairman (5) and (6), Fries (7), Lindau (9), De Notaris (10), Peck (12), Saccardo (14), (15), and (17), Schweinitz (17), and Thumen (19). Macroscopic observations were made of all the following species except Caryospora coffeae. These specimens were examined either at the United States Department of Agriculture mycological herbarium or at the mycological herbarium of the New York City Botanical Garden. The following species of Caryospora have been described:

# 1. C. CALLICARPA (Curr.) Nitschke & Fuckel.

Perithecia large, 34–1 mm., subglobose, papillate and ostiolate. Asci ovate-clavate, 210– $260 \times 60$ – $70 \mu$ , eight-spored. Spores large, 87– $108 \times 30$ – $47 \mu$ , uniseptate with one or two small loculi at each end. Occurs in North America on dead oak wood and on bark of *Populus nigra*.

# 2. C. CARIOSA Fairman.

Perithecia large, conic, black, ostiolate, mainly superficial. Asci oblong-cylindrical,  $150 \times 20 \mu$ , 2–8-spored. Spores  $36-43 \times 13-17 \mu$ , occasionally with extra septa near the ends. Occurs in North America on beech wood.

# 3. C. COFFEAE Pat.

Perithecia subglobose, black 0.5–1 mm., ostiolate. Asci club-shaped,  $200-250 \times 45-60 \,\mu$ , 8-spored. Spores  $80 \times 20 \,\mu$ , first uniseptate then five septate. Occurs on twigs of coffee trees in Venezuela.

## 4. C. Langloisii Ellis & Ev.

Perithecia slightly sunken, nearly 1 mm. wide, brownish-black, distinct ostiole, papilliform. Asci 120–140  $\times$  40–45  $\mu$ , 8-spored. Spores 1-septate, somewhat constricted, 35–45  $\times$  16–20  $\mu$ . Occurs in Louisiana on old canes of *Arundinaria*.

## 5. C. LICHENOPSIS (Mass.) Sacc.

Perithecia ½ to ¾ mm. in height. Asci 150–170  $\times$  15–20  $\mu$ , 8-spored. Spores about 8-septate, 34–36  $\times$  12–14  $\mu$ . Occurs in Italy on bark of living *Cerasus*.

### 6. C. MINOR Peck.

Perithecia 350–500  $\mu$  in height, conic, and ostiolate. Asci subcylindrical,  $150 \times 20~\mu$ , 4 to 8-spored. Spores contain one median septum and sometimes 3 to 5 pseudosepta,  $45–50 \times 12~\mu$ . Occurs in North America on pericarp of hickory nuts.

## 7. C. NUCLEARIA Thüm.

Perithecia 1 mm., carbonaceous, broad, and ostiolate. Asci elongate, 8-spored. Sporidia elongate, somewhat constricted, 4-loculate. Occurs in Italy on old olive pits.

## 8. C. OLEARUM (Cast.) Sacc.

Perithecia  $\frac{3}{4}$  mm. in height, conic, and ostiolate. Asci 110–140  $\times$  12–15  $\mu$ , 8-spored. Spores  $28-32 \times 9-10.5 \mu$ , 5 to 7 septate. Occurs in Italy on bark of *Olea europea*.

# 9. C. PUTAMINUM (Schw.) De Not.

Perithecia 0.5 to 1.2 mm. in height, black, carbonaceous, papillate, and ostiolate. Asci clavate,  $200-350 \times 50-75 \,\mu$ , 2 to 8-spored. Spores  $60-150 \times 35-65 \,\mu$ , median septate with 1 to 5 loculi at each tip. Occurs mainly on old peach stones.

While examining peach stones for Caryospora putaminum, another form of this genus was found which differed from any of the species described above. The perithecia are black, carbonaceous in texture, and ostiolate. Perithecia vary from 400 to 750  $\mu$  in height and are usually about as broad as they are high. Asci are cylindrical-clavate,  $150\text{--}180 \times 35\text{--}50 \,\mu$ , and are always eightspored. These spores are light brown in color, median septate and usually possess one small septum at each tip. The tips are somewhat rounded. The average size of these spores is  $45 \times 24 \,\mu$ . Ellis and Everhart (4) mentioned the occurrence, on peach stones, of an organism which they believed to be an eight-spored

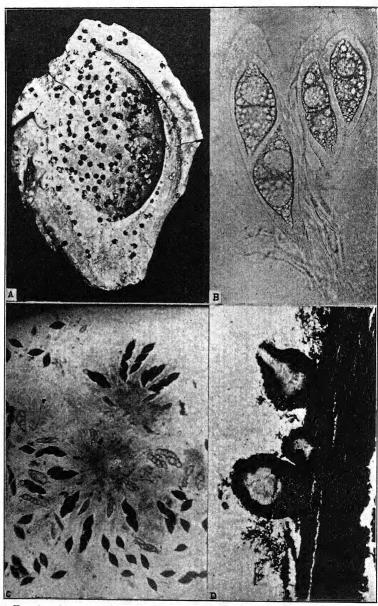


Fig. 1. Caryospora putaminum. A, perithecia on peach stone,  $\times$  2.5; B, two-spored asci,  $\times$  420; C, partial contents of a mature perithecium,  $\times$  90; D, spermagonia produced in culture,  $\times$  120.

form of *C. putaminum*. As they gave no further description and as this organism differs from the other known species of *Caryospora*, it is proposed as a new species.

## Caryospora minima sp. nov.

Peritheciis sparsis, nigris, conicis, ostiolato,  $400-700~\mu$  altis; ascis clavatocylindraceis,  $150-180~\mu$  longis  $\times$  35-50  $\mu$  crassis, 8-sporis; sporidiis  $40-50~\mu$  longis  $\times$  20-30  $\mu$  crassis, obtusus, uniseptatis, ad septum leniter constrictis, unoloculus ad extremitis, subfuscus. Habitat in putamine putrescente Amyg-dalus~persica in Maryland.

Type collected at Berlin, Maryland, August 1938, and deposited in the Mycological Collections of the Bureau of Plant Industry (No. 71132). Other collections were made at College Park and at Conway Station, Anne Arundel Co., Maryland. Portions of the type collection also deposited in the herbarium of the New York Botanical Garden, the Farlow herbarium of Harvard University, and the herbarium of the University of Michigan.

Single-spore isolations were made, and cultures were grown on various media. On peach-stone agar the mycelium is dark grey in color while the substrate is black. Perithecia are produced in culture but not very abundantly. The growth requirements of this fungus were almost identical with those of *C. putaminum*. Perithecia were produced over a pH range of 4.75 to 6.51. Peaextract agar caused cultures of *C. minima* to become lighter in color, but neither spermagonia nor sclerotia were found.

Perithecia of *C. minima* are identical with those of *C. putaminum* except for the difference in size. The perithecial wall is made up of similar pseudoparenchymatous tissue while asci and paraphyses arise from a layer of hyphae in the base of the perithecium. During moist weather spores are exuded through the circular ostiole and form a compact mass on top of the perithecium.

Asci of C. minima are usually produced by crozier formation (FIG. 2, A, B). Occasionally asci arise directly from a branch of the ascogenous hyphae without crozier formation. Crozier formation is much more frequent in this species than in C. putaminum. The fusion nucleus in young asci of C. minima is about  $3.8 \mu$  in diameter with a dense nucleolus of  $2.3 \mu$ . The ascus elongates until it is about two-thirds full size; then the dense cytoplasm be-

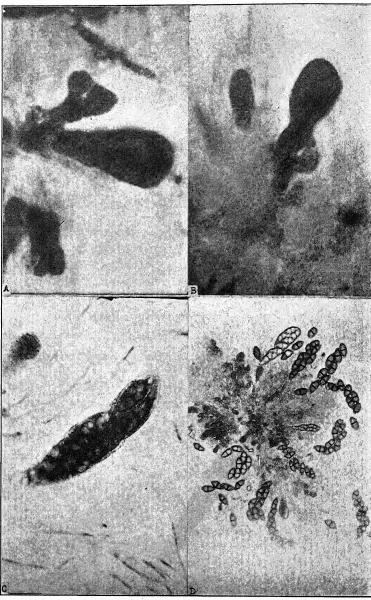


Fig. 2. Caryospora minima. A, early stage of crozier formation,  $\times$  2000; B, later stage of crozier formation,  $\times$  2000; C, ascus containing recently delimited ascospores,  $\times$  450; D, asci containing mature ascospores,  $\times$  150.

comes vacuolate and eight spores are delimited by the process of free cell formation (FIG. 2, C). Spores are at first hyaline and contain one median septum; each of the two cells thus formed contains one nucleus. As the spores mature, the color becomes light brown and a septum appears at each tip. Each spore is surrounded by a very thin hyaline layer which disappears upon drying. Asci and spores of *Caryospora minima* are shown in figure 2, D.

The mycelium of Caryospora minima is very similar to that of Caryospora putaminum, being brown in color, sparsely septate, and averaging about  $2.5 \mu$  in diameter. Most of the mycelial cells appear uninucleate, but the nuclear condition is often difficult to determine due to the many nuclear-like chromatin bodies which occur in the cells. Anastomoses occur frequently in young mycelium.

#### DISCUSSION

Caryospora putaminum differs from most Pyrenomycetes in that it forms various numbers of spores per ascus. Other fungi of this order form less than eight spores per ascus, but the number of spores usually remains constant. However, in *C. putaminum* the number of spores per ascus may range from one to seven, but an eight-spored ascus has not been observed.

Saccardo (16) made the only reference so far noted to the occurrence of spermagonia and spermatia in *Caryospora putaminum*. His description is as follows:

"Fungus spermogonium spermatiis minutissimis cylindraceis, oscillantibus." Saccardo's idea of movement by the spermatia was probably due to Brownian movement or surface tension phenomena, for no evidence of self-propulsion has been noted.

The only reference to the proposed *Caryospora minima* was made by Ellis and Everhart (4). They noted that such a fungus did exist but did not propose it as a separate species; their complete description is as follows:

"Occasionally a peach pit is met with, on which all the perithecia produce 8-spored asci, but in this case the sporidia are smaller,  $30-50\times18-20~\mu$ . There are generally but two of the larger sporidia in an ascus."

Evidently they considered it as merely an eight-spored form of *Caryospora putaminum* and did not take into consideration the difference in perithecial size and spore shape. In *C. putaminum* perithecia always contain asci with varying numbers of spores per ascus, but in *C. minima* there are always eight spores per ascus.

Several workers doubt the validity of the genus Caryospora. Ellis and Everhart state that it is hardly more than a subgenus of Trematosphaeria. Peck (12) states that Caryospora minima may be a Melanomma or a Trematosphaeria. Höhnel (8) and others have noted the similarity between the genera Sphaeria and Trematosphaeria. The main source of confusion in the classification of Caryospora are the small septa which are usually found at the tip of each spore. The number of terminal septations per spore is variable and in some instances they are not even present. It seems that Caryospora constitutes a distinct genus but that its position in the Sphaeriaceae should be changed. Due to its terminal septations, Caryospora is now placed in the Phaeophragmiae, but as true cells are not formed by these septa, it seems likely that this genus should be included in the Phaeodidymae.

Tassi (18) reported the occurrence of an organism which he believed to be the pycnidial stage of *Caryospora putaminum*. He called this organism *Santiella putaminum* and described it as follows:

Peritheciis sparsis, globoso-conicis, papillatis, subcarbonaceis, nigris, subsuperficialibus, basi insculptis, facile secedentibus, 200–250  $\mu$  diam., sporulis breve fusoideis, medio 1-septatis, intense fuligineis, non constrictis, crasse 2-guttalis, utrinque locello copuliformi V. obtusulo hyalino auctis 22–26  $\times$  12.

He found this species in Italy on old stones of *Prunus domestica*. Tassi also reported another similar organism on old seeds of *Melia Azedarach*; this he called *Santiella oblonga*. Saccardo (16) also mentions these species, but he only repeats Tassi's description.

#### SUMMARY

- 1. Best growth and production of perithecia of *Caryospora putaminum* occurred when cultures were grown at 25–28° C. on malt agars adjusted within the pH range of 5.0–6.0.
  - 2. Growth on pea-extract agar differed in color from that on

malt-extract agar. Spermagonia and spermatia occur readily on the former with perithecia occurring only occasionally; on malt agar perithecia occur readily while spermagonia and spermatia are only of occasional occurrence.

- 3. Spermatia do not appear to be absolutely necessary for sexual reproduction and apparently are not concerned in dissemination.
  - 4. Asci arise with or without crozier formation.
- 5. The most common number of spores per ascus is three, but from one to seven may occur.
- 6. A young three-spored ascus was observed to contain one nucleus per spore with five nuclei remaining in the epiplasm. Apparently the nucleus included in each spore divides and a median septum forms which gives rise to a two-celled ascospore, each cell of which contains one nucleus.
- 7. Most mycelial cells are uninucleate, but some appear to be multinucleate.
- 8. Division figures in paraphyses indicate a chromosome number of three or four.
- 9. Caryospora minima is proposed as a new species. It differs from other species of this genus mainly in spore size and shape.
- 10. Asci of *Caryospora minima* arise mainly by crozier formation and contain eight ascospores when mature. Each spore has two main cells and contains one nucleus per cell.

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# PHOTOGRAPHS AND DESCRIPTIONS OF CUP-FUNGI—XXXV. A NEW SPE-CIES OF PATELLA

FRED J. SEAVER

(WITH 1 FIGURE)

For several years past the writer has been collecting, on burned areas in The New York Botanical Garden, a small brown *Patella* which superficially resembles *Sphaerospora brunnea*, but can at once be distinguished from this species by its ellipsoid spores. It was at first thought to be a dark colored form of *Patella melaloma*, but again is strikingly different in color and also has stubby, bristly hairs instead of the adpressed, blunt hairs which are so characteristic of *P. melaloma*.

After puzzling over this species for several seasons, the writer has finally decided to describe it since nothing has been encountered to which it could be referred.

# Patella contradicta sp. nov.

Apothecia sessile, thickly gregarious or usually densely crowded, early becoming subdiscoid with the margin scarcely elevated, brown, reaching a diameter of 1–2 mm., rarely slightly larger, clothed about the margin with an inconspicuous fringe of hairs; hymenium plane or slightly concave, same color as the outside of the apothecium; hairs relatively short, bristly, tapering into a rather sharp tip, usually consisting of several cells, the basal one strongly swollen and subglobose, hyaline or subhyaline, usually not exceeding 50–80  $\mu$  in length and often much shorter; asci cylindric or subcylindric, reaching a length of 125–160  $\mu$  and a diameter of 12–16  $\mu$ , 8-spored; spores usually 1-seriate, broad ellipsoid, usually containing 2 oil-drops, about 10 ×12–16  $\mu$ ; paraphyses enlarged above the tips reaching a diameter of 5  $\mu$ .

Apotheciis, sessilis, dense gregariis, orbicularis, brunneis, 1–2 mm. diam. margine pilis erectis, brevibus, hyalinis, erectis obsita; hymenio subplano

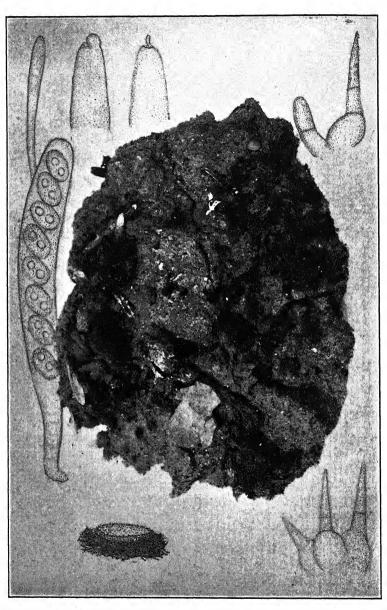


Fig. 1. Patella contradicta.

brunneo; asciis cylindraceis vel subcylindraceis, 8-sporiis, 12–16  $\times$  125–160  $\mu$ ; sporiis ellipticis 10  $\times$  12–16  $\mu$ ; paraphysibus clavulatis, 5  $\mu$  diam.

On soil where wood has been burned.

Type locality: The New York Botanical Garden. Distribution: Known only from the type locality.

NEW YORK BOTANICAL GARDEN

# NOTES AND BRIEF ARTICLES

NORTH AMERICAN FLORA

The final part of Volume 7 of North American Flora has recently appeared. Volume 7 consists of a monograph of the rusts and smuts of North America. The final part consists of a Bibliography by John Hendley Barnhart, and General Index by Gussie Mildred Miller. Mycologists have long complained that this volume, comprising more than a thousand pages, was not readily usable without the index, and the appearance of this part will doubtless be much appreciated by them. Full details may be had on request.—Fred J. Seaver.

## Mounting Fluids and Double Cover-Glass Mounts

In a recent account presenting in detail a most commendable standardization of my method of mounting microscopic preparations between two cover-glasses Dr. Chupp 1 has proposed the name 'Shear's mounting fluid' for a formula associated by some persons with the name of Dr. C. L. Shear. This gives a certain nomenclatorial status to the formula (2 per cent potassium acetate in water 300 cc.; glycerine 120 cc.; 95 per cent ethyl alcohol 180 cc.). There is an equally useful formula of which the above appears to be an adaptation, and in view of my personal experience with the technique referred to, as well as familiarity with the media previously utilized, I feel obligated to present some historical details as pertinent.

'Shear's mounting fluid' described by Chupp actually differs slightly from that with which I had been familiar, and which has been used for years by many persons in Washington as a medium for semi-permanent mounts. This latter formula, presumably much older, is as follows: potassium acetate 10 grms.; water 500

<sup>&</sup>lt;sup>1</sup> Chupp, C. Further note on double cover-glass mounts. Mycologia 32: 269-270. 1940.

cc.; glycerine 200 cc.; 95 per cent ethyl alcohol 300 cc. This medium with just enough copper sulfate added to give it a light-blue tint made possible very satisfactory temporary preparations, but ringed mounts of from five to ten years old were observed in 1920 to be filled with blackish flecks that rendered them useless; the flecks were apparently of precipitated metallic copper. After 1921 the medium did not include the copper. It had also been customary to add to this medium small amounts of certain compatible stains (erythrosin, eosin, light-green, etc.) which had proved a suitable means of staining and preserving fungous structures at one operation. When in 1925 Colley 2 published this older formula and standardized the amount of erythrosin used he added as a footnote: "The medium has been used for years in the Bureau of Plant Industry, by Dr. C. L. Shear and others. The only modification of their formula is the addition of the erythrosin." I actually supplied Dr. Colley with the formula from the label of the stock bottle in the mycological laboratory. He had searched for a previous record of it, but without avail. Likewise several years earlier I had developed a lively curiosity with respect to the origin of this formula and its proper name. Search in the usual literature was fruitless and personal inquiries of my associates resulted in no definite answer. In 1921 I was told by Mrs. Flora W. Patterson, in charge of the Mycological Collections from 1896 to 1923, that she thought she had obtained it from Dr. C. L. Shear or from Mr. A. B. Seymour. When Dr. Shear was asked he replied that he had obtained it from Mrs. Patterson! I was told at a much later date by Mr. Seymour that he had never heard of this formula.

What name or whose name ought to be applied to this older formula still in use in Washington laboratories? The name 'Shear's mounting fluid' is preëmpted by the later modification and can not apply to it. It is possible that some obscure record of it may later be found but until that time it is only fitting to call it 'Patterson's mounting medium.'—WILLIAM W. DIEHL.

<sup>&</sup>lt;sup>2</sup> Colley, R. H. A biometric comparison of the urediniospores of *Cronartium ribicola* and *Cronartium occidentale*. Jour. Agr. Res. 30: 283–291. 1925.

## NOTES ON GYMNOSPORANGIUM IN OKLAHOMA

In the spring of 1939 the author, with the aid of others, gathered together numerous collections of species of *Gymnosporangium* affecting various members of the genus *Juniperus* in Oklahoma. Several of these collections proved interesting in that new hosts and new localities for described species of the rust on Juniper were discovered. Because of these facts a list of some of the collections is hereby presented. Specimens of nearly all collections are deposited in the Mycological Herbarium, United States Department of Agriculture, Washington, D. C.

# 1. Juniperus virginiana L.

- a. Gymnosporangium clavipes C. & P.—Collected April 6, 1939 and May 8, 1939, in Stillwater. Arthur <sup>1</sup> does not list this fungus in Oklahoma.
- b. Gymnosporangium globosum Farl.—Collected March 26, 1939, at Stigler. This species is not so common as G. Juniperivirginianae.
- c. Gymnosporangium Juniperi-virginianac Schw.—Collected March 26, April 5, and May 8, 1939, in Stillwater. Evidently the commonest cedar rust in the state, especially since the host is native and commonly used for ornamental purposes and windbreaks.
- d. Gymnosporangium Nidus-avis Thaxt.—Collected at the College Nursery on a dozen trees, May 8, 1939. These collections proved to be a problem, for the spores were borne in flat, irregularly-shaped horns arising from small, gall-like excrescenses along the branches. Such a habit is not usual. The spores were unusual and consisted of 2–4 cells. The several-celled spores had two pores near the septa of each cell except the uppermost cell which had the pore arranged apically. Specimens were sent to Dr. Kern for identification. Although no positive determination was made, he suggested that the rust was G. Nidus-avis, pointing out that this species was variable in habit and in the number of cells in each spore. Further study may reveal this fungus as new. Oklahoma is not listed as a locality for this rust by Arthur.<sup>1</sup>

<sup>&</sup>lt;sup>1</sup> Arthur, J. C. Manual of the rusts in United States and Canada. p. 1-438. 1934.

### 2. Juniperus virginiana var. Canaertii Sénécl.

a. Gymnosporangium Juniperi-virginianae Schw.—Collected March 26, 1939, at Stigler.

## 3. Juniperus virginiana var. glauca Carr.

a. Gymnosporangium Juniperi-virginianae Schw. — Collected March 26, 1939, at Stigler.

## 4. Juniperus virginiana var. globosa Beiss.

- a. Gymnosporangium Juniperi-virginianae Schw. Collected March 26, 1939, at Stigler.
- b. Gymnosporangium floriforme Thaxter.—Collected April 6, 1939, at Stillwater.

## 5. Juniperus virginiana var. pyramidalis Carr.

a. Gymnosporangium Juniperi-virginianae Schw.—Collected March 26, 1939, at Stigler.

## 6. Juniperus chinensis var. Pfitzeriana Spaeth.

a. Gymnosporangium Juniperi-virginianae Schw.—Collected March 26, 1939, at Stigler. This rust is not recorded on this host by Arthur.<sup>1</sup>

## 7. Juniperus scopulorum Sarg.

a. Gymnosporangium Betheli Kern.—Collected March 26, 1939, at Stigler. This fungus represents the first collection of G. Betheli in the state.

## 8. Juniperus mexicana Spreng.

a. Gymnosporangium exiguum Kern.—Collected April 7, 1939, in the Arbuckle Mountains. The host in this state is confined strictly to the region of the Arbuckles. Nearly every tree of the several hundred examined was infected in some degree. No tree, however, appeared to suffer any ill-effects from the presence of the rust. The identification of the rust was confirmed by Dr.

Kern. This report of the fungus in Oklahoma is the first. This host remains immune to *G. Juniperi-virginianae*, even though many trees of *Juniperus virginiana* affected by the rust are common in the same area with it. Because of this immunity to the destructive cedar-apple rust, nurserymen in the state are recommending the use of Mexican Juniper in place of the red cedar.—W. Winfield Ray.

#### FINANCIAL STATUS OF MYCOLOGIA

During the year 1939 the total receipts for Mycologia were \$4384.16, and the total expenditures \$3749.69, leaving an accumulated balance of \$1055.43. Of this amount, most of which was from the sale of back sets, \$1000 was added to the Mycologia Endowment Fund, bringing it up to a total of \$7000.

During the present year, 1940, the expenditures for Mycologia must increase with the gradual expansion of the publication, while the income is being reduced to some extent through the loss of foreign subscriptions, resulting from the war conditions in Europe. All our present income will, therefore, probably be required to continue Mycologia at its present pace. To make up for the loss of foreign subscriptions we must look to the increase in the membership of our Mycological Society of America at home. Every member is, therefore, urged to use his influence to secure one additional member during the year in order that we may continue our activities unabated.—Fred J. Seaver.

# **MYCOLOGIA**

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No. 5

## INTERESTING SPECIES OF LACTARIAE FROM FLORIDA

H. C. Beardslee and Gertrude S. Burlingham

(WITH 4 FIGURES)

The following species of Lactariae have been collected by the authors for several fall and winter seasons in various localities in Orange and Seminole counties, Florida.

Lactaria floridana sp. nov. (Fig. 1, A; 4, A)

Pileus fleshy, firm, umbilicate with arched incurved margin, at length spreading and deeply depressed in the center, up to 12 cm. broad; surface varying from brownish terra cotta 1 to cinnamon or buff or pale buff with the center ochraceous to maize yellow, azonate or sometimes faintly zoned, very viscid when young even in dry weather, tomentose on the margin and half way to the center or sometimes up to the disc with long tangled agglutinated fibres which do not project beyond the margin as in Lactaria torminosa; context firm, thick, white to pale yellowish flesh, aromatic with pleasant odor remaining when dried; latex white, unchanging, scanty, very acrid; lamellae nearly white at first, becoming pale ecru tone 4 singly, then near honey-yellow tone 1, and finally ochroleucous on the edges, and isabelline tone 1 in position, unequal, mostly simple with a few forking near the stipe, broad in the outer half, narrowed toward the stipe and attached with a decurrent tooth, close; stipe pale blush to cinnamon tone 1 or tinted with it, becoming maize tone 4 with age, pruinose at the apex, sometimes with small scrobiculate spots at base or on the

<sup>1</sup> Unless otherwise noted the colors used are those of the Repertoire de Couleurs.

[Mycologia for July-August (32: 419-574) was issued August 1, 1940]

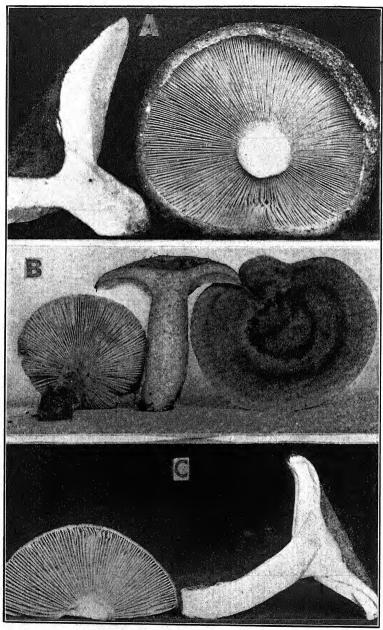


Fig. 1. A, Lactaria floridana  $\times$  1, often larger; B, Lactaria cognoscibilis  $\times$  1; C, Lactaria impercepta  $\times$  1.

lower half, nearly equal, from 2–4 cm.  $\times$  1.4–2.3 cm., firm, solid; spores pale blush tone 1–2 to pale yellowish flesh tone 2 in thick mass, 5–5.5–6.25  $\mu \times$  6.87–7.5–8.75  $\mu$ , uniguttulate and apparently smooth under the  $\frac{1}{6}$  power without iodine, but under oil immersion with iodine they are seen to be reticulate with scattered protuberances, unsymmetrical, apiculate.

Pileo carnoso, firmo, umbilicato, margine arcuato et incurvato, demum expanso et centro profunde depresso, colore variabili, e brunneo-latericeo (322) cinnamoneo (323) aut isabellino (309) et centro ochraceo, azono aut leviter zonato, primo viscossisimo etiam siccitate, margine aut ad medium fibris longis agglutinatisque tomentosis sed non ut in *Lactaria torminosa* exstantibus; carne firma, crassa, alba, pallide lutescente, odoro grato aromaticoque etiam siccata; lacte albo, immutabili, exiguo, acerrimo; lamellis primo subalbis demum pallide lutescentibus (66 t-4), simplicibus aut paucis ad stipitem furcatis; stipite e carneo-albo (137) cinnamoneo, apice pruinoso, basi interdum leviter scrobiculato, subaequali; sporis e incarnato-albis (137 t 1–2) luteolo-albis (68 t-2), 5–5.5–6.25  $\mu$  × 6.87–7.5–8.75  $\mu$ , uniguttulatis, minute echinulatis et lineis delicatis reticulatis.

Type Locality: On Route 24 about three miles north of Apopka, Orange Co., Florida.

Habitat: In sandy soil in rather open live oak and pine woods, Dec. and Jan.

This species differs from Lactaria scrobiculata (Scop.) Fries in its unchanging latex and scarcely zonate pileus; from Lactaria torminosa (Schaeff.) Pers. it differs in the character of the tomentum on the margin which is agglutinated on the surface and does not form a fringe on the edge and in the very small protuberances on the spores. Also in the coloration both in the field and when dried it does not resemble that species. Some specimens were found in places which had been lightly burned over a few months before.

## Lactaria cognoscibilis sp. nov. (Fig. 1, B; 4, B)

Pileus broadly convex becoming plane to a little centrally depressed, sometimes with a small sharp umbo, 3.5 to 8.5 cm. broad; surface mineral brown tone 1 or paler zoned with deeper tones, with a white pruinose bloom at first, dull, fading and becoming azonate, a little viscid when wet; margin arched but finally upturned and remaining pruinose for some time; context near dark fawn, decidedly peppery and lasting; latex white, unchanging, abundant, bitter then slowly peppery, more quickly and intensely peppery in young specimens; lamellae pale flesh tone 4 singly, unequal, sometimes forking near the stipe, adnate with a slightly de-

current tooth, interveined next the pileus, pruinose when mature, close; stipe paler than the pileus, pruinose, nearly equal but abruptly smaller at the base, solid 3–3.5 cm.  $\times$  .7–1.2 cm.: spores fleshywhite tone 3 in thick mass, broadly elliptical to globose, coarsely echinulate with some connecting bands, apiculate, 7.5–8  $\times$  8–8.75  $\mu$  or 8.75  $\times$  8.75  $\mu$  or 8.75  $\times$  8.75  $\mu$ .

Pileo e late convexo, expanso aut subdepresso, interdum acute subumbonato, 3.5–8.5 cm. lato, minerale-brunneo (339) aut pallidiore et zonis orscurioribus notato, demum pallidiore et azono, primo leniter albo-pruinoso udo viscidulo, diu pruinoso; carne fusca fulva (307), diu acerrima; lacte albo, immutabili, abundante, amaro et tarde acri, aetate juniore acriore; lamellis pallide incarnatis (136 t-4) inaequalibus, paucis ad stipitem furcatis, adnatis et dente subdecurrentibus demum pruinosis, confertis; stipite pileo pallidiore, pruinoso, subaequali basi abrupte constricto, solido, 3–3.5 cm.  $\times$  .7–1.2 cm.; sporis albidulis (9 t-3) late ellipticis aut subglobosis, valde echinulatis et reticulatis, apiculatis, 7–8  $\times$  8–8.75  $\mu$  ad 8.7  $\times$  8.7  $\mu$ .

Type Locality: The Black Hammock, Oviedo, Florida.

HABITAT: In black sandy humus under sweet gum with live oaks and cabbage palms near, often gregarious.

DISTRIBUTION: Widely scattered in the type locality, also in a hammock near Green Springs, Volusia Co., Florida.

This species resembles *Lactaria mutabilis* Peck in color and zonation but can quickly be distinguished by the bitter peppery taste of the latex. It is common in the hammocks where found, from November through January when the weather is not too cold or dry. In large drops the latex seems to separate into milky and clear.

## Lactaria proximella sp. nov. (Fig. 2, A; 4, C)

Pileus broadly convex-umbilicate, then expanding and shallowly infundibuliform, brownish-terra-cotta tone 2 zoned with tone 4, to cinnamon, whitish pruinose in the center, viscid when wet, 2.5 to 6 cm. broad; margin arched, at length uplifted and more or less fluted, sometimes striate; context paler than the lamellae but not pure white, odor none, wounds especially in the stipe may turn glaucous after some time where the latex has dried; latex white unchanging, scanty, very peppery; lamellae nearly white at first becoming chamois colored to cinnamon tone 1 singly, unequal, some forking near the stipe, broader than the flesh, slightly decurrent, close; stipe paler than the pileus, isabelline to maize tone 3-4, nearly equal except spreading a little at the apex, pruinose when young, 1.3-2 cm. × .8-1 cm.; spores fleshy white tone 2 to pale

blush tone 1–4, 7.5–8  $\mu \times 9.4 \mu$ , echinulate under the  $\frac{1}{6}$  power but with iodine stain and oil immersion the echinules are connected by bands, apiculate, unsymmetrical.

Pileo late convexo-umbilicato demum expanso et subinfundibuliformi, brunneo-latericeo (322 t-2) obscurioribus zonis notato, ad cinnamoneum, centro albo-pruinoso, udo viscido, 2.5 to 6 cm. lato; margine arcuato demum recurvato, flexuoso, interdum striato; carne lamellis pallidiore, inodora, vulnerata interdum glaucescenti; lacte albo, immutabili, exiguo, acerrimo: lamellis primo subalbis, tum e pallidis cinnamoneis, aequalibus, paucis ad stipitem furcatis, carne latioribus, subdecurrentibus, confertis; stipite pileo pallidiore, subaequali sed apice leniter incrassato, primo pruinoso, 1.3–2 cm.  $\times$  .8–1 cm.; sporis albidulis (9 t-2), 7.5–8  $\mu$   $\times$  9.4  $\mu$ , echinulatis et reticulatis.

Type locality: Oak woods on the shores of Lake Wildmere, Longwood, Florida.

Habitat: Under black and live oaks in sandy soil, from November into January.

DISTRIBUTION: In various localities in the type woods, also under scrub oaks in the scrub near the Apopka airport, and in the hammock at the Fort Christmas Land Development Co., near Fort Christmas, Orange Co., Florida.

This species resembles Lactaria insulsa Fries in color but is much smaller, less zonate, and the wounds in the stipe often turn green, and the spores are smaller. From Lactaria zonaria Fries it differs in the less viscid scarcely zonate or azonate pileus, smaller size, lack of odor and the smaller spores. According to Rea the lamellae of Lactaria zonaria sometimes "become dingy or even somewhat aeruginous when bruised." The change of color in Lactaria proximella occurs chiefly on wounds of the stipe. From Lactaria coleopteris Coker it differs in lack of odor, less viscidity, lack of the white collar at the apex of the stipe, and the larger spores. Since this species is plainly rather closely related to all the species of this group, yet differs from each, the specific name seems appropriate.

## Lactaria limacina sp. nov. (Fig. 2, B, C; 4, E)

Pileus umbilicate with inrolled margin becoming infundibuliform, up to 9 cm. broad; surface tinted snuff brown tone 1 when young, then tone 2 to putty color or chamois tone 1 when mature, azonate, slimy viscid with cuticle separable nearly one-half way to the center, glabrous to within about one cm. of the margin; margin

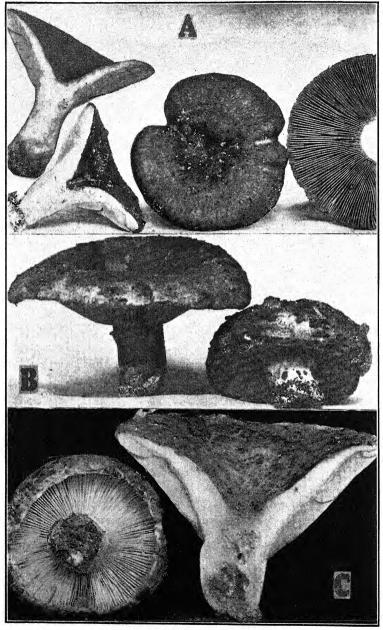


Fig. 2. A, Lactaria proximella  $\times$  1; B, C, Lactaria limacina  $\times$  1.

with agglutinated tangled tomentum with short fibres projecting from the involute edge; context pale yellowish flesh tone 1, or with a tint of snuff brown, odor none; latex white unchanging, slowly very peppery; lamellae whitish at first, becoming putty color singly and dark fawn in position, unequal, a few forking near the stipe, narrow at the inner end and slightly decurrent, close; stipe whitish at first then putty color, solid, sometimes scrobiculate, slimy, 1.7 to 2 cm.  $\times$  1 cm. to 1.8 cm. at the apex and 1.3 to .8 cm. at the base: spores fleshy-white tone 2 to 3, coarsely echinulate with echinules of different sizes connected by lines or bands of varying widths, apiculate, 8–8.75  $\mu \times 10~\mu$ .

Pileo umbilicato, margine incurvato, demum infundibuliformi, Havannabrunneo (303 t-1) tum pallidiore, azono, viscoso, pellicula margine separabili, disco glabro sed margine involuto fibris agglutinatis projecantibusque tomentose; carne pallide luteo-incarnata (68 t-1), aut brunneo tincta, inodoro; lacte alba, immutabili, tarde acerrimo; lamellis albidis tum luteolis (311), inaequalibus, paucis ad stipitem furcatis, postice angustatis, subdecurrentibus, confertis; stipite ex albido luteola (311), solido interdum scrobiculato, viscoso, 1.7–2 cm. × 1–1.8 cm. apice, basi leniter constricto: sporis albidis (9 t-2 to 3), inaequaliter echinulatis et reticulatis, 8–8.75  $\mu$  × 10  $\mu$ .

Type locality: Rock Springs (Kelly Park), Orange Co., Florida.

Habitat: In humus under live and water oaks.

DISTRIBUTION: Rock Springs and Longwood, Florida.

This species is characterized by its short stipe, slimy pileus with the agglutinated fibrous marginal area, and the unchanging white acrid latex. Rarely a specimen was found with some spots on the surface of the pileus giving it a subzonate appearance. The fibrous margin and the color separate it from *Lactaria hysgina* Fries, and the unchanging color of the latex on the wounds is an additional characteristic separating it from *Lactaria trivialis* Fries. The spores are also paler than in either of these species.

## Lactaria impercepta sp. nov. (Fig. 1, C; 4, F)

Pileus from broadly convex spreading and slightly umbonate, 5.5 cm. broad; surface dark fawn to snuff brown tone 2, azonate, viscid when wet, glabrous; margin becoming striate on the edge when mature; context staining sulphur yellow when cut, without odor; latex white, slowly becoming sulphur yellow, bitter, then peppery; lamellae pallid, tinted rosy-white tone 4 singly, broad and rounded at the outer end, narrowed toward the inner and a little

decurrent, unequal, sometimes forked at the stipe, close; stipe pale flesh tone 4, 3.5 cm.  $\times$  1 cm. at the apex to .8 cm. at the base which is white tomentose, solid: spores fleshy-white tone 1, 8.7–9  $\mu \times$  10–11.25  $\mu$ , reticulate with small protuberances, apiculate, unsymmetrical.

Pileo e lato convexo expanso, subumbonatoque, 5.5 cm. lato, fuscefulvo (307 to 303 t-2), aut Havanna-brunneo (303), azono, viscido udo, glabro; margine demum striato; carne vulnerata lutescente, inodora; lacte albo, tarde sulphurescente (18), amaro, tum acri; lamellis subincarnatis (8 t-4), latis, exto rotundatis, ad stipitem attenuatis, subdecurrentibus, inequalibus, interdum ad stipitem furcatis, confertis; stipite pallide incarnato (136 t-4), 3.5  $\times$  1 cm., deorsum constricto et albo-tomentoso, solido; sporis albidis (9 t-1) 8.7–9  $\mu \times$  10–11.25  $\mu$ , tuberculeis-reticulatis, apiculatis inequalibus.

Type locality: Black Hammock opposite the flowing sulphur well, near Oviedo, Florida.

HABITAT: In a hammock of sweet gum, maple and oaks.

DISTRIBUTION: In type locality and in woods three miles from Apopka on the road to Rock Springs, Florida.

This species seems to be rare but it may be because it has been overlooked. It differs from Lactaria cognoscibilis in being azonate and in the changing color of the latex and cut flesh and in the larger more reticulate spores. From Lactaria theiogala (Bull.) Fries it differs in the more slender form, azonate pileus, less crowded lamellae, more slowly changing latex and absence of odor. In fact in the field it would not suggest any of these species.

## Lactaria pseudodeliciosa sp. nov. (Fig. 3, A; 4, G)

Pileus broadly convex, deeply umbilicate, expanding and infundibuliform, 6 to 8.5 cm. broad; surface nearly white becoming with age over the central portion putty color tone 1 to ochroleucous or maize tone 2 to pale buff, azonate to faintly zonate, very viscid when wet; margin thin, agglutinated fibrous under the lens, easily visible when young; context without odor, turning drab green where wounded; latex neutral orange, scanty, slowly peppery; lamellae honey yellow tone 1 singly except at the base which is orange and gives orange tones to the lamellae in position, unequal, interveined, some anastomosing at the base, adnate to adnate-decurrent; stipe isabelline tone 1–4, somewhat scrobiculate, white tomentose on the lower half, short, solid, 1.2 cm.  $\times$  1 cm. to 2.5 cm.  $\times$  2 cm., extending to a root-like point on one side: spores maize 2–3, 6.87– $7.5 \mu \times 8.75$ – $9 \mu$ , reticulate and minutely tuberculate, unsymmetrical, apiculus small.

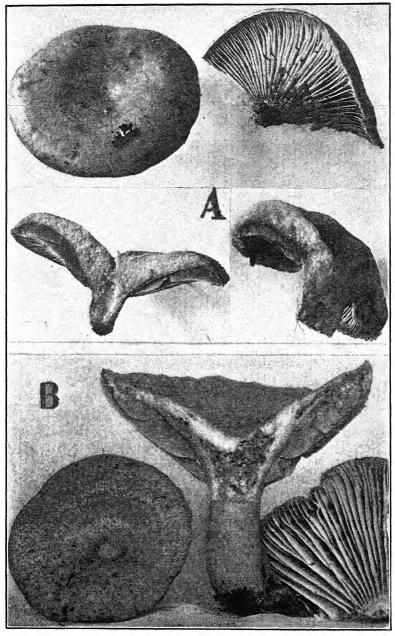


Fig. 3. A, Lacturia pseudodeliciosa  $\times$  1, often larger; B, Lacturia paradoxa  $\times$  1.

Pileo late convexo, profunde umbilicato, tum expanso, et infundibuliformi, 6–8.5 cm. lato, subalbo, disco e pallido ochroleuco, azono aut interdum leviter zonato, viscosissimo; margine tenui, minute fibrillis agglutinatis tomentoso; carne inodora, vulnerata virescente; lacte exiguo, aurantiaco, tarde acri; lamellis melleis, basi aurantiacis, inaequalibus, intervenosis, paucis basi cohaerentibus, adnatis aut adnato-decurrentibus; stipite isabellino, leniter scrobiculato, infra albo-tomentoso, curto, solido,  $1.2 \times 1$  cm. ad  $2.5 \times 2$  cm., basi unilatere acuto-constricto pseudo-radicanteque:sporis pallide luteis (36 t 2–3), tuberculis et reticulatis,  $6.87-7.5~\mu \times 8.75-9~\mu$ .

Type locality: Rock Springs, (Kelly Park), Orange Co., Florida.

Habitat: Under laurel leaved oaks and long leaf pine in a rather open place where the sun could reach during some part of the day.

DISTRIBUTION: Rock Springs, near Oviedo, Longwood and New Smyrna, Florida.

This species seems closely related to *Lactaria deliciosa* (L.) Fries from which it differs in the agglutinated fibrous edge as seen with a lens, the nearly white and usually azonate pileus, the lack of odor, the smaller more finely echinulate spores connected by finer lines, and the small apiculus. In the field the pileus is practically white before it begins to age.

## Lactaria paradoxa sp. nov. (Fig. 3, B; 4, H)

Pileus fleshy, broadly convex becoming centrally depressed and at length infundibuliform, grayish indigo to smalt blue zoned with darker tones, with a silvery sheen over all, fading with age, very viscid when wet, glabrous, 5.2 cm. to 8 cm. broad; margin thin even, showing a tint of the latex when mature; context with a tinge of mahogany-red due to the latex, odorless; latex mahoganyred, a little bitter or astringent, then slowly a little peppery; lamellae putty color to cinnamon singly, in position showing a tint of corinthian red due to the latex, becoming green where injured, unequal, a few forking near the stipe, adnate to decurrent, broad, brittle, easily bleeding; stipe tinged slate violet to smalt blue at the base, equal or tapering downward, and at the base tapering into a root-like extension, 2-3 cm.  $\times$  1.2-1.5 cm. at the apex to .8 cm. above the root-like projection; spores pale ecru tone 4 to maize tone 2 in deep mass, broadly elliptical, reticulate with rather broad bands and with small protuberances of unequal sizes, 6.87-7.5  $\mu$  $\times$  8–9  $\mu$ .

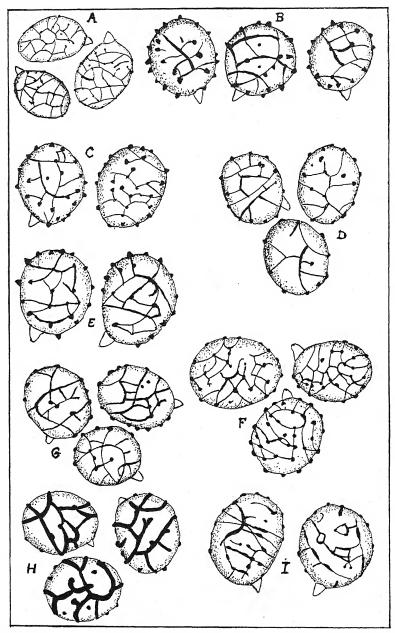


Fig. 4. Spores of A, Lactaria floridana; B, L. cognoscibilis; C, L. proximella; D, L. torminosa from specimens collected in Sweden; E, L. limacina; F, L. impercepta; G, L. pseudodeliciosa; H, L. paradoxa; I, L. subpurpurea.

Pileo carnoso, late convexo, demum centro depresso et infundibuliformi, caeruleo (232 ad 209), obscurioribus zonis, demum aetate pallidiore, udo viscosissimo, glabro, 5.2 ad 8 cm. lato; margine tenui, laevi; carne lacte colorato, inodoro; lacte fusco-rubro (335), subamaro aut astricto tum tarde acri; lamellis e luteolis (311) cinnamoneis (323) aut lacte rubescentibus, vulneratis virescentibus, inaequalibus, paucis ad stipitem furcatis, adnatis deinde decurrantibus, latis, fragilibus, lacte faciliter plurantibus; stipite supra livido (173) basi caeruleo (209), aequali aut infra constricto et subradicante, 2–3 cm.  $\times$  1.2–1.5 cm.; sporis pallide luteis (66 ad 36 t-2), late ellipticis, latis lineis parvis tuberculis late reticulatis 6.87–7.5  $\mu$  × 8–9  $\mu$ .

Type Locality: Fort Christmas Land Development Co. hammock at "Old Faithful," near Fort Christmas, Florida.

Habitat: In somewhat grassy places under cabbage palmetto and live oaks in a fairly shady spot in rich soil, or in lawns having similar conditions.

DISTRIBUTION: In the type locality and in a lawn at Altamonte Springs, Florida.

When viewed from above in its habitat it closely resembles Lactaria Indigo (Schw.) Fries, but upon looking at the under side one is surprised to find it closely resembles Lactaria subpurpurea Peck, and the latex is mahogany red instead of blue as one would expect from the color of the upper side of the pileus. The spores differ in size and shape and markings from those of Lactaria subpurpurea (Fig. 4, I). The spores of the latter species are larger, and the bands are not of uniform width and are more tuberculate.

The spore drawings in figure 4 were made with the aid of a camera lucida, using a 1/12 oil immersion lens and a 15 mm. ocular giving a magnification of about 1500.

## THE GENUS MYRIANGIUM IN NORTH AMERICA

JULIAN H. MILLER 1

This interesting group of plectomycetous fungi occur on scale insects which parasitize various woody plants. They are distributed over the entire world, but are especially common in the southern United States.

The plant body consists of a black pseudoparenchymatous stroma, which later gives rise to a peculiar type of apothecium with an apically delimited fertile region, consisting of asci at different levels embedded in coalesced fungous tissue. The ascospores are liberated by the gelatinization of the surface layer followed by the elongation of the asci, a transverse splitting of the ascal wall, and a forceable expulsion of the spores. There is apparently no conidial stage. The development of the fruiting body has previously been described by the writer (6).

The stroma is superficial on the bark and no mycelium has been found in live tissue. Directly under each stroma are several dead scales, penetrated and covered by mycelium. There is a definite relationship between the death of the scale and that of the limb and the *Myriangium*. No live stromata have been discovered on dead branches

There is apparently some host specificity as regards both the scale and the tree, but in most of the herbarium specimens studied it has been impossible to identify the scale. In the United States the two commonest species are *Myriangium Duriaei* and *Myriangium asterinosporum*, and the former was on every black gum observed by the writer and the latter on nearly every hawthorn. On the other hand these species have also occasionally been found on other hosts, but no cases have been observed where they crossed hosts.

<sup>&</sup>lt;sup>1</sup> The author wishes to express his appreciation to Dr. F. J. Seaver, The New York Botanical Garden, Dr. D. H. Linder, Harvard University, and Dr. C. W. Dodge, Missouri Botanical Garden, for the loan of specimens.

Records in North American literature of scale insects acting as hosts include the following: Aspidiotus perniciosus, Chionaspis biclavis, Chionaspis Citri, Chionaspis sylvatica, Diaspis pentagona, Lepidosaphes Becki, Lepidosaphes Gloveri, Lepidosaphes Ulmi, Mytilaspis citricola, and Parlatoria Pergandei. Most of these have been determined on Citrus species in Florida or the West Indian Islands, and the fungus has in most cases been wrongly determined as Myriangium Duriaei.

Species of *Myriangium* are important in control of scale insects, and have been so cited by South (14) and Johnston (3) for the West Indies, and by Fawsett (2) for Florida.

#### HISTORICAL REVIEW

Petch (12) in 1924 has given a most complete review of the literature of Myriangium. Berkeley received specimens from Australia, and on submitting them to Montagne found that he already had collected a similar fungus in the Department of Eastern Pyrenees in France, and had received another one from Algeria. So they (9) published the description under joint authorship in 1845. Apparently Berkeley wrote the diagnosis and Montagne (7) the next year published a second description and illustrations. Two species were described under the genus, Myriangium Duriaei and Myriangium Montagnei. The first then becomes the type, and is based on the Montagne collection in the Pyrenees, and the second is from the Australian collection.

In 1849 Berkeley received specimens from M. A. Curtis in South Carolina, which he sent to Montagne (10) and the latter then emended the genus and published a third species, *Myriangium Curtisii*.

Both Berkeley and Montagne placed *Myriangium* among the lichens in the family Collemaceae. This was probably due to the greenish tint sometimes found in *Myriangium Duriaei*, and to the disc shaped apothecia and muriform spores, somewhat similar to those of *Collema*. However, there are no internal algal components, although one does occasionally find some algal cells, chiefly *Protococcus*, on the surface of an old stroma.

Nylander in "Synopsis methodica Lichenum" in 1858 erected

a family Myriangiaceae with a tribe Myriangiei, and included the two species, Myriangium Duriaei and Myriangium Curtisii.

In the United States, Tuckerman in "Genera Lichenum" in 1872 shows that Myriangium Duriaei of Europe is equal to Myriangium Curtisii of America. Later in 1882 he (16) lists Myriangium Duriaei (Mont. & Berk.) Tuck., and cites as synonyms Myriangium Duriaei Mont. & Berk. and Myriangium Curtisii Mont. & Berk. There was no reason for this transfer of a species already in the genus. This inclusion in the lichens by Tuckerman was followed by many North American collectors.

Millardet (5) was one of the first to recognize the relationship with the fungi and placed the family Myriangiaceae near the Tuberaceae.

The writer (l.c.) in 1938 summarizes the question of the relationship of *Myriangium* species. The fact that the single ascal locule is formed from ascogenous hyphae clearly indicated a close affinity to the Gymnoascales.

#### SYSTEMATIC ACCOUNT

Myriangium Mont. & Berk. London Jour. Bot. 4:72. 1845. Emended Mont. Ann. Sci. Nat. III, 11:245. 1849. Phymatosphaeria Pass. Nuov. Giorn. Bot. Ital. 7:138. 1886. Pyrenotheca Pat. Bull. Soc. Bot. Fr. 33:155. 1886.

Stroma superficial, black with lighter colored interior, orbicular to irregular, no free mycelium; apothecia few to many seated on the stroma and consisting of a differentiated fertile layer with asci at different levels above a sterile region; asci globose to subglobose, with 8 spores; ascospores elliptical to oblong, muriform, hyaline to subhyaline.

On Coccidae on woody plants.

The genus is limited to the original concept of a stroma with many apothecia parasitizing scales and superficial on the bark. Such plant parasites as *Diplotheca tunae* (Spreng.) Starb., although placed in *Myriangium* by Petrak (13) differ sufficiently in lacking the flat basal stroma and in parasitism to warrant the retention of *Diplotheca*. The only other species described from North America, *M. Sabaleos*, by Weedon (17) does not belong in the *Myriangium* connection.

The use of the term apothecium for the fruiting body of Myriangium is questionable, but seem preferable to such terms as perithecium or cleistothecium, which have been applied to other plectomycete forms as those in Aspergillus or Penicillium. The asci in Myriangium push up through the ascogenous hyphae at maturity, and the fertile region is fully exposed, which is different from the situation in Aspergillus. There one finds a sterile crust entirely inclosing the asci and the spores are liberated only after the decomposition of the peridium. The only distinction between the exposed ascal region in Myriangium and that of a typical discomycete lies in monostichous asci in the latter and polystichous ones in the former, and that doesn't seem sufficient to warrant coining a new term.

Petch (l.c.) observed some globose spores in several species of *Myriangium*, but the writer has found only oblong-elliptical ones in parts of the same specimens he examined. The spherical shape appears only in cross sections of spores as shown by the figures of the writer (l.c.).

#### KEY TO NORTH AMERICAN SPECIES OF MYRIANGIUM

Fertile region arising from the inside of a marginate, disc-shaped, stalked apothecium, with concave line separating it from the stroma.

1. M. Duriaei.

Fertile region superficial from the first, both upper and lower lines more or less parallel and convex to flat; apothecia emarginate.

Apothecia well differentiated on a discrete stroma, 1-2 mm. high.

Apothecia sessile, rounded, or truncate when crowded, scarcely raised above the surface of a flat indefinite stroma. . . . . 4. M. floridanum.

1. Myriangium Duriaei Mont. & Berk. London Jour. Bot. 4:72. 1845.

Myriangium Curtisii Mont. & Berk. Ann. Sci. Nat. III. 11: 245. 1849.

Type: Specimen in Montagne herbarium on *Morus alba*, collected in France in 1830.

Stroma black with pale interior, fleshy to gelatinous when wet, flat to convex, orbicular, plicate-radiate, 1.5–5 mm. in diam.; few to many apothecia arising as erect processes with depressed center, with fertile region in the upper part, at first closed, but fully ex-

posed at maturity, disc-shaped, stalked, .5–1.5 mm. in diam. and .5–1 mm. high, with distinct margin, surface plane or convex becoming concave with drying or discharge of spores; asci globose to semiglobose, 35–50  $\mu$  in diam., with thick hyaline wall, 8-spores; ascospores oblong-elliptical, muriform, constricted at middle septum, 7–9 transverse septa and 1–3 longitudinal divisions, subhyaline, 25–36  $\times$  12–14  $\mu$ .

In North America it is most common on Nyssa sylvatica and Nyssa biflora, but also occurs on Heteromeles arbutifolia, Liquidambar Styraciflua, Magnolia virginiana, and Quercus nigra. In Europe the collections are chiefly on Fraxinus excelsior, and Morus alba and in Africa on Laurus nobilis. The distribution of the species is apparently world wide.

ILLUSTRATIONS: Petch (l.c.) pl. II, f. 1-4, sub M. Duriaei, and f. 6 sub M. Curtisii, and pl. III, f. 1-4. The f. 4 is named M. Curtisii, but is a typically expanded M. Duriaei. Miller (l.c.) f. 4, 1-5.

The apothecia of Myriangium Duriaei in most herbarium specimens are either immature or else old and disintegrated. This is due to the fact that in the absence of a prolonged wet period they fail to develop and may remain in an arrested condition of rudimentary tubercules for many months, and so the periods in which they can be collected in the mature state is very brief. Petch (l.c.) describes these initials as well as open apothecia without drawing the conclusion that the former are only immature stages of the latter.

The North American form on *Nyssa* is fully equal to the European specimens cited below. The Italian specimen *n.* 27 is old, but has typical concave cups with definite borders. The English specimen from Currey on *Fraxinus* is the best developed one of the foreign collections in the New York Botanical Garden herbarium.

Petch (l.c.) cites the New Jersey specimen n. 143 and the Ravenel collection n. 332, all on Nyssa, as typical of this species, which is in agreement with this paper.

#### MATERIAL EXAMINED

#### United States

- Curtis Collections, Harvard Univ., M. Duriaei Mont. & Berk. on Nyssa, South Carolina. M. Duriaei on Nyssa, S. C., ex herb. C. D. Faxon. M. Duriaei on Nyssa, S. C., det. R. Thaxter. M. Curtisii Mont. & Berk. E. Tuckerman herb., ex Michener, Chester, Pa., 1852. 2 specimens. (Probably co-type of M. Curtisii.)
- Ravenel Collections, M. Curtisii Mont. & Berk., South Carolina, Apr. 1859, ex Tuckerman herb., 2 specimens. M. Curtisii, S. C., ex Gray herb. M. Curtisii, on Nyssa, Santee Canal, S. C., 1849, Harvard herb. M. Curtisii, on Nyssa, S. C., Mo. Bot. Gard. herb. no. 34895. M. Curtisii, on Nyssa, Aiken, S. C., Rav. Fungi Am. 332, 2 specimens. N. Y. Bot. Gard.
- Ellis Herb., M. Duriaei Mont. & Berk., on Nyssa, Newfield, N. J., May 25, 1900. Harvard herb. M. Duriaei, on Nyssa, Newfield, N. J., 2 specimens, n. 23, N. Y. Bot. Gard. herb. 143. M. Duriaei, on Nyssa multiflora, Acto, N. J., H. A. Green, 3 specimens in N. Y. Bot. Gard. herb. and 2 in Mo. Bot. Gard. herb. 270. M. Duriaei, Charleston, S. C., Apr. 1895, H. A. Green. M. Duriaei, Chester, S. C., H. A. Green, N. Y. Bot. Gard. herb. M. Duriaei, on Nyssa, Takoma Park, Md., Mar. 1900, ex herb. T. A. Williams. 1060. M. Curtisii, on Nyssa multiflora, Wilmington, Del., Oct. 1889, ex herb. A. Commons. N. Y. Bot. Gard. herb.
- Calkins Collections, 35. M. Duriaei, Florida, June 17, 1903, N. Y. Bot. Gard. herb. 66. M. Duriaei, Lookout Mt., Tenn., N. A. Lichens. 74. M. Duriaei, Cook Co., Ill., N. A. Lichens, Harvard herb. 136. M. Duriaei, Lookout Mt., Tenn., N. A. Lichens, Mo. Bot. Gard. herb.
- Earle, F. S. 2241. Dothiora asterinospora Ellis & Ev., on Nyssa, Auburn, Ala., Jan. 16, 1897, N. Y. Bot. Gard. herb.
- Faxon, C. D. M. Duriaei, Kaiser, W. Va., Dec. 12, 1880, Harvard herb.
- Hasse, H. E. 270. M. Duriaei (Mont. & Berk.) Tuck., on Heteromeles arbutifolia, Santa Monica, Calif., 1898. N. Y. Bot. Gard. herb., also 2 specimens in Harvard herb.

- Linder, D. H. & R. F. Smart. M. Duriaei, on Nyssa sylvatica, Richmond, Va. Harvard herb.
- Rapp, S. 14. Myriangium sp., Sanford, Fla., on Magnolia virginiana, Dec. 25, 1907. 174. M. Duriaei, Sanford, Fla., 1910. Harvard herb.
- Miles, L. E. 777. M. Duriaei, on Liquidambar Styraciflua, Auburn, Ala., Apr. 1923. Harvard herb.
- Thaxter, R. 4108. M. Duriaei, West Palm Beach, Fla., Jan. 2, 1897. det. Petch. 4109 is a duplicate. Harvard herb.
- Weir, J. R. & W. W. Diehl. M. Curtisii, on Nyssa sylvatica, Fosteria, Va., Mar. 4, 1932. Harvard herb.

In addition to the above the writer has collections from Georgia on Nyssa biflora, Nyssa sylvatica, Liquidambar Styraciflua, and Quercus nigra.

#### South America

Thaxter, R. 4106. M. Duriaei. Corral, Chile, Dec. 1905. det. Petch. 4107 is a duplicate. Harvard herb.

## Europe

Roumeguere, C. 9. M. Duriaei, Lichenes Gallica exsicc.

Desmazieres, J. B. & H. J. M. Duriaei, Plantes Crypt. de France.

Solis, A. L. M. Duriaei, Urville, Hague pres Cherbourg, 1857.

Richard, O. J. M. Duriaei, Lichens of Cherbier, Mar. 1879. On Fraxinus excelsior, Vezuley. 2 specimens.

Currey, W. M. Duriaei, on Fraxinus excelsior, Apr. 1876.

Massalongo, A. B. 27. M. Duriaei, Lichens Italici exsicc.

The above are all in the New York Botanical Garden herbarium.

## Africa

- Maire, R. 45. M. Duriaei, on Laurus nobilis, Aonidia Lauri Bouche, Feb. 1912, Mycotheca Boreali-Africana. N. Y. Bot. Gard. herb.
- Myriangium asterinosporum (Ellis & Ev.) comb. nov.
   Cenangium asterinosporum Ellis & Ev. Bull. Torrey Club 10:
   76. 1883.

Dothiora asterinospora Sacc. Syll. Fung. 8: 766. 1889. Type: Ellis herb. no. 1279, on Vaccinium corymbosum.

Stroma black, flat at first, later hemispheric, orbicular, radiate-plicate on the margin, yellow inside, superficial, 2–5 mm. in diam., and 1–2 mm. high; apothecia many on stroma, usually leaving no free margin, sessile, orbicular to angular when crowded, .1–.8 mm. in diam., chiefly .4 mm., discrete, slightly elevated, black, with wide base, convex to flat; fertile region occupying upper portion of apothecium, exposed from the first; asci semiglobose to globose,  $35–52~\mu$  in diam.; ascospores 8, oblong-elliptic,  $25–34~\times~9–14~\mu$ , muriform, constricted at middle septum, 7–9 septate and with 1–3 longitudinal divisions, hyaline to light yellow.

Hosts: Chiefly on Crataegus spp., but also found on Acer, Amelanchier, Cyrilla racemiflora, Ilex decidua, Ilex lucida, Ilex verticillata, Malus angustifolia, Malus pumila, and Vaccinium corymbosum.

DISTRIBUTION: Apparently limited to the United States and Canada, especially the eastern parts.

ILLUSTRATIONS: Miller (1.c.) f. 4, 6, 7.

This species was designated *M. Curtisii* by the writer (l.c.) in 1838, and also by Petch (l.c.) in part, but recent investigations lead to the conclusion that Montagne had both of the common American species before him and combined the two in his description of *M. Curtisii*.

The type of *M. Curtisii* is a Curtis specimen collected in South Carolina and sent to Berkeley. According to Petch (l.c.) Berkeley forwarded this one on to Montagne, and the latter described it under joint authorship. Also, Petch says there is no specimen in the Berkeley herbarium labelled *M. Curtisii* by Berkeley, and that in the Montagne herbarium there is one labelled *M. Curtisii* Mont. & Berk. in Broome's handwriting with "Mont. Ann. Sci. B. t. 12, 1849," added by Montagne, which is *M. Duriaei*. Then there is another specimen marked by Montagne "Myr. Curtisii B. & M. Car. Inf. Amer. Boreal," which Petch says has the large apothecia of *M. Curtisii* and is probably the type. However, this cannot be determined with any degree of certainty as Montagne did not cite either a number or the host in his description.

In the Farlow Herbarium at Harvard there is a specimen from Curtis labelled *M. Curtisii* from the Tuckerman herbarium, which should be the cotype. This is on *Nyssa* and has large apothecia, and is distinctly *M. Duriaei*. Then Montagne in Sylloge Plant.

Cryptogamarum p. 381 cites both Curtis and Ravenel as sources of *M. Curtisii*, and the Ravenel specimens under that name in the Harvard herbarium, the New York Botanical Garden herbarium, and in the Missouri Botanical Garden herbarium are all on *Nyssa* and are *M. Duriaei*.

The Montagne description of *M. Curtisii* is also confusing. In regard to the apothecia he (10) says, "... sesselia, haud adnata, elevato-marginata, scutelliformia, concaviuscula..., disco subconcolori...," and earlier under the *M. Duriaei* description there is "Apothecia tuberculiformia primo clausa, tanden aperta plana immarginata." The common form on *Crataegus*, or the Thaxter specimen on *Amelanchier*, which Petch determined as *M. Curtisii*, has no elevated margin, is never concave, and disc is not concolorous but black. Therefore, as both descriptions fit *M. Duriaei*, and the Curtis and Ravenel specimens named *M. Curtisii* are in reality *M. Duriaei*, the Ellis name *asterinosporum* becomes the first to be applied to this species.

Ellis and Everhart (1) recognized only one species in North America, M. Duriaei, and placed Cenangium asterinosporum and M. Curtisii in synonymy.

The spore measurements given by Ellis and Everhart for M. asterinosporum are  $15{\text -}20 \times 6{\text -}8~\mu$  with 3 septa, and Petch says the spores are  $16{\text -}19 \times 7~\mu$ , with some spherical ones  $18~\mu$  in diam. These are probably measurements of immature spores as older parts of the Ellis type have spores as given above by the writer.

This species is included in part by Petch (l.c.) under the name *M. Curtisii*. He separates the two common species as follows:

"Stroma at first green internally:

ascigerous region cup-shaped

1. Myr. Duriaei

Stroma yellow-brown internally:

asci in a zone parallel to the surface

2. Myr. Curtisii"

The above key contains the essential elements separating the two species, but Petch gives as an illustration of M. Curtisii a photomicrograph of a section through a typically expanded form of M. Duriaei. Also, he cites under M. Duriaei the Ellis specimen, Cenangium asterinosporum, which is exactly the same as the one on Amelanchier at Harvard that he determined as M. Curtisii.

#### MATERIAL EXAMINED

- Anderson, F. W. M. Curtisii Mont. & Berk., on Acer, Newfield, N. J., May 1890. N. Y. Bot. Gard. herb.
- Bartholomew, E. 1101. M. Duriaei, on Crataegus, Iowa City, Ia., May 1905, U. S. D. A. Myc. Coll. Mo. Bot. Gard. herb. and Harvard herb. [Collected by F. J. Seaver]
- Burke, R. P. 7. Myriangium sp., Fungi of Montgomery Co., Ala., N. Y. Bot. Gard. herb.
- Dearness, J. 1141. M. Duriaei, on Crataegus, London, Can., Nov. 1903. Ellis & Ev. Fungi Columb. N. Y. Bot. Gard. herb.
- Earle, C. F. Dothiora asterinospora Ellis, on Cyrilla racemiflora, Auburn, Ala., Jan. 1891. N. Y. Bot. Gard. herb.
- Ellis, J. B. 1081. Cenangium asterinosporum Ellis, on Vaccinium corymbosum, Newfield, N. J., Dec. 1882; no. 1279 collected Apr. 1883; an unnumbered one, May 23, 1883. N. Y. Bot. Gard. herb. No. 1279 also in Harvard herb.
- Fitzpatrick, H. M. 14763. M. Duriaei, on Crataegus, McLean, N. Y., July 1925. Harvard herb.
- Greene, H. A. M. Duriaei (Mont. & Berk.) Tuck., Tryon, N. C., 1899, det. Merrill. Harvard herb.
- Honey, E. E. & Jenkins, A. E. 69635. M. Duriaei, on Crataegus, McLean, N. Y., 1927. N. Y. Bot. Gard. herb.
- Jackson, H. S. 6075. M. Duriaei, on Crataegus, N. of Erindale, Ont., Oct. 1933. Harvard herb.
- Martin, G. W. M. Duriaei, on Crataegus, North Liberty, Ia., Apr. 7, 1934. N. Y. Bot. Gard. herb.
- Norton, J. B. S. 2503. M. Duriaei, on Crataegus, Webster, Md., Oct. 1889. Mo. Bot. Gard. herb.
- Overholts, L. O. 58213. M. Duriaei, on Crataegus, Rock Springs, Pa., May 1921. Mo. Bot. Gard. herb.
- Piquet, A. P. D. M. Curtisii, Sharon, Mass., det. Thaxter. Harvard herb.
- Sheldon, J. L. 2874. M. Duriaei, on Crataegus Crus-galli, Marillo, W. Va., May 20, 1907. Harvard herb.
- Thaxter, R. 623. M. Curtisii, on Amelanchier, Tyler City, Conn., Oct. 1888, det. Petch. N. Y. Bot. Gard. herb. Duplicates, nos. 623, 4105, 3864, Harvard herb. 776. M. (Duriaei) Curtisii,

on Cocci on Amelanchier, Harvard herb. Myriangium sp., on Ilex verticillata, New Haven, Conn., 1888, Harvard herb.

The writer has Georgia collections on Crataegus Collina, C. Crus-galli, C. Michauxii, C. spathulata, and C. uniflora; and one on C. punctata from Ithaca, N. Y. Other Georgia collections are on Ilex decidua, Malus angustifolia and Malus punila.

3. Myriangium tuberculans Miles, Mycologia 14: 80. 1922. Type: Specimen on *Carya Pecan*, in herb. L. E. Miles, Agr. Coll. Miss.

Stroma at first flat, later hemispheric, black, light pinkish-brown inside, orbicular, discrete, radiate-plicate on margin, 1–4 mm. in diam. and 1–2 mm. high; apothecia orbicular to irregular, flattened to convex, .1–.4 mm. high, usually not distinct, but part of a continuous branching system of convolutions occupying the entire stroma, with peripheral fertile regions covering all exposed surfaces; asci semiglobose, 35–55  $\mu$  in diameter; 8 spores, oblong-elliptic, with obtuse ends, 7-septate, with 1–2 longitudinal divisions, subhyaline,  $25–32\times10–14~\mu$ .

On scale insects on Carya Pecan, Carya alba, and Carya sp. in southern United States.

ILLUSTRATIONS: Miles (l.c.) pl. 14, f. 1-4.

The apothecia are not as distinct as in M. asterinosporum, but in all other characters there is a marked similarity. The fertile region is convex with parallel lines in sections, and exposed from the first as in the other species. The chief difference lies in the pinkish color of the interior of the stroma in contrast to the light yellow of M. asterinosporum. Also the stromal texture remains firm, and does not crumble with age as in the latter.

Petch (l.c.) places this form under M. Curtisii (M. asterino-sporum of this paper), but the writer thinks the difference in stromal color is sufficient to maintain a separate species.

#### MATERIAL EXAMINED

Miles, L. E. 115. M. tuberculans, on Carya Pecan, Pascagonla, Miss., May 8, 1921. M. tuberculans, on Carya Pecan, Ocean Springs, Miss. N. Y. Bot. Gard. herb. 785. Myriangium sp. on pecan, Selima, Ala., Mar. 10, 1923. Harvard herb.

Demaree, J. B. 1544. M. Duriaei, on Carya Pecan, Putney, Ga., Mar. 15, 1922, Harvard herb. and Mo. Bot. Gard. herb.

In the writer's herbarium this species is on Carya Pecan, Carya alba, and Carya sp. from Georgia.

4. Myriangium floridanum Höhnel, Sitz-ber. Akad. Wiss. Wien. 118: 354. 1909.

Type: Specimen on Citrus Aurantium, Umatilla, Fla., Rehm herbarium, ex Ellis.

Stroma very thin, flat, indefinitely effused, following the contours of the bark, externally black and light straw colored inside; apothecia isolated or crowded, sessile, elevations pulvinate, hemispheric to truncate, .1–.3 mm. high and .3–.6 mm. in diameter, surface black pulverulent, with no free margin; fertile region convex with asci semiglobose to globose, 35–53  $\mu$  in diam.; ascospores 8, oblong-elliptic, with 7–9 septa and 1–2 longitudinal divisions, subhyaline, 27.6–32  $\times$  9.2–12  $\mu$ .

On various scale insects on Citrus Aurantium, Citrus nobilis var. Unshiu, Citrus Limonia, and on Gleditsia triacanthos. Found in southern United States, the West Indies, and Africa.

The specimens on *Citrus* species studies by the writer are similar in possession of imperfectly developed emarginate apothecia, completely sessile on the flat basal stroma, with the fertile region not sharply defined. This is in distinct contrast to the cup-shaped apothecia of *M. Duriaei*, or the apothecia of the other species with their raised sterile stroma under each fertile region.

M. floridanum is the most primitive species and is not far removed from some of the more highly developed forms in Elsinoe.

The form on *Gleditsia* has been found only in the Mississippi valley states. It does not differ sufficiently from the specimens on *Citrus* to warrant the creation of a separate species. These minor variations consist in a slightly thicker stroma and more indefinite apothecial elevations.

#### MATERIAL EXAMINED

#### United States

Dozier, H. L. *M. Duriaei*, on *Citrus nobilis* var. *Unshiu*, Mobile, Ala., Apr. 7, 1923, det. W. W. Diehl. *809*. *M. Duriaei*, on purple scale on Satsuma orange, Loxley, Ala., Apr. 10, 1923. Harvard herb.

- Ellis herb. *M. Duriaei*, on orange, Umatilla, Fla., C. W. Hopkins, with drawings by E. A. Southworth. N. Y. Bot. Gard. herb. 778. *M. Duriaei*, on orange twigs, Florida, det. Thaxter. Harvard herb. ex Ellis.
- Savage, F. 1547. M. Duriaei, with Mytilaspis Citri on Citrus trifoliata, Eustis, Fla., Jan. 1902. U. S. D. A. Myc. Coll. Mo. Bot. Gard. herb., Harvard herb. and N. Y. Bot. Gard. herb.

#### West Indies

- Britton, N. L. 13291. M. Duriaei?, on Pseudocarpidium Wrightii, at Palm Barren, Santa Clara, Cuba, Apr. 8, 9, 1912. N. Y. Bot. Gard. herb.
- Greene, J. 1546. M. Duriaei, with Mytilaspis citricola & Chionaspis citri, on lemon twig, Oriente, Cuba, Nov. 29, 1909. U. S. D. A. Myc. Coll. Harvard herb., Mo. Bot. Gard. herb., and N. Y. Bot. Gard. herb.
- Seaver, F. J. & Chardon, C. E. 343. M. Duriaei, on oyster shell scale, Puerto Rico. 1660. M. Duriaei, on scale insect, Rio Portugues n. of Ponce, Explor. of P. R. n. 395. 2081 M. Duriaei, Jan. 24, 1923, Explor. of P. R. n. 1071. 1983. M. Duriaei, Explor. of P. R. n. 718, on Bromeliad. N. Y. Bot. Gard. herb.
- Seaver, F. J. 3435. M. Duriaei, on insect, Plants of Trinidad, Br. W. I., Apr. 3, 5, 1921. N. Y. Bot. Gard. herb.

## Africa

Humber, T. M. Duriaei, on orange, Coomassie, Gold Coast, Africa, 1917. Harvard herb.

#### UNITED STATES

#### On Gleditsia

- Ellis Herb. 4067. M. Duriaei Mont. & Berk., on Gleditsia triacanthos, Fountain Bluff, Ill., May, 1894. Rab.-Wint.-Pazsch. Fungi Europaei. N. Y. Bot. Gard. herb.
- Langlois, A. B. 94. M. Curtisii Mont. & Berk., on Gleditsia, Point a la Hache, La. Dec. 8, 1885. Flora Ludoviciana. M. Cur-

tisii, on Gleditsia, St. Martinsville, La., Apr. 15, 1895. N. Y. Bot. Gard. herb.

Miles, L. E. Myriangium sp., on Gleditsia triacanthos, Miss. A. & M. College, Apr. 4, 1922. N. Y. Bot. Gard. herb.

Tracy, S. M. 182. M. Curtisii, on Gleditsia triacanthos, Starkville, Miss., Mar. 1, 1889. Mo. Bot. Gard. herb. and N. Y. Bot. Gard. herb.

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- 4. Miles, L. E. A new species of Myriangium on pecan. Mycologia 14: 77-80. 1922.
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- 8. —. Syll. Plant. Crypt. pp. 380-1. 1856.
- 9. & Berkeley, M. J. London Jour. Bot. 4: 72. 1845.
- 10. & —. Ann. Sci. Nat. III 11: 235–246. 1849.
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- Petch, T. Studies in entomogenous fungi. V. Myriangium. Trans. Brit. Myc. Soc. 10: 45-80. 1924.
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- South, F. W. The control of scale insects in the British West Indies by means of fungoid parasites. W. I. Bull. 11: 1-30. 1910.
- 15. Tuckerman, E. Genera Lichenum. p. 141. 1872.
- 16. —. Synopsis of North American Lichens. p. 261. 1882.
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   1926.

## ANGULAR LEAF SPOT OF PITTOSPORUM

A. G. PLAKIDAS

(WITH 4 FIGURES)

In June, 1938, Mr. L. A. Hetrick, then with the State Department of Agriculture, sent from New Orleans specimens of *Pittosporum* (*P. tobira*) leaves showing very striking yellowish-brown angular spots (Fig. 1, *A*). Examination of the specimens showed fungus mycelium within the spotted leaf tissue and sporophores (apparently those of *Cercospora*) protruding in fascicles from the stomata. A few spores were also present. No published account or description of the disease was found. Later, the disease was found on *Pittosporum* shrubs on the University campus, and in gardens in Baton Rouge, New Orleans, Thibodaux, and other places in southern Louisiana and along the Mississippi coast.<sup>1</sup>

#### DESCRIPTION

The spots are characteristically angular (Fig. 1, A) and chlorotic, but usually not necrotic. Completely necrotic spots occur only rarely. The invaded tissue remains alive for a long time. For example, leaves infected by artificial inoculation in May, 1939, still showed chlorotic but no necrotic spots on January 8, 1940, about seven months after the appearance of the spots. It is true that if the tissue of even relatively young spots is sectioned and examined with the microscope, groups of necrotic spongy parenchyma and palisade cells are found, chiefly in the vicinity of fungus mycelium, but, on the whole, the invaded tissue remains alive. This is a very interesting feature of this particular disease, for fungi of this genus (Cercospora) usually behave as aggressive parasites, killing the host tissue and causing necrotic spots shortly after infection has taken place. In the early stages, the spots are pale green in

<sup>&</sup>lt;sup>1</sup> Recently Dr. G. F. Weber informed the writer that the disease described in this paper is present in Florida. Press Bulletin 520, with the title "Leaf Spot of Pittosporum," by E. West, released by the Florida Agr. Exp. Sta. in August, 1938, came to the writer's attention recently.

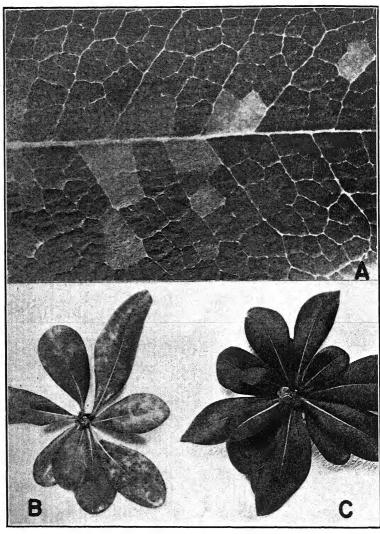


Fig. 1. Angular leaf spot of  $Pittosporum\ tobira$ . A, portion of a leaf showing typical angular chlorotic spots,  $\times$  5; B, shoot showing very severe symptoms, with more than one-half of the leaf area covered with chlorotic spots; C, healthy shoot for comparison. B and C approx.  $\frac{1}{2}$  nat. size.

color and hardly discernible unless viewed through transmitted light. Later, the spots become distinctly chlorotic, and still later yellowish-brown on the upper and olive brown on the under surface. Solitary spots may vary from 1 to 5 mm. in size. Coalescing spots are much larger, often covering more than one-half the area of the leaf (Fig. 1, B), but even the large coalescing spots have angular margins. The angularity of the spots is due to the fact that the spread of the fungus through the tissue is checked, temporarily at least, by the veinlets, so that the margins of the spots follow the outline of the veinlets. It is only rarely that a spot may show a diffuse margin.

Mycelium occurs in the affected tissue between both the spongy parenchyma and the palisade cells. It is especially abundant directly under the lower epidermis where it forms a rather dense growth in the sub-stomatal air spaces (FIG. 2), from which the sporophores arise and protrude through the stomata (FIG. 3, A).

The disease occurs on both the green and the variegated varieties of Pittosporum. In general, it is not a serious disease, for, although some spotting may be found on practically every Pittosporum shrub in certain areas, it is relatively seldom that the infection is severe enough to cause serious damage. However, many individual shrubs have been noted that were so heavily spotted as to present a chlorotic, sickly, unsightly appearance (FIG. 1, B). It often happens that a severely-diseased shrub may be growing next to, or between, other shrubs that show only an occasional spot, and the disease does not seem to spread to them, although the cultural and environmenal conditions appear identical for all. No satisfactory explanation can be offered at present for this apparent difference in susceptibility. As far as it could be determined, all the Pittosporums growing in the region under observation belong to the same species (P. tobira), and, since they are propagated vegetatively, all plants should be the same, unless clonal mutations in respect to susceptibility occur. Furthermore, when old plants which showed only occasional spots were inoculated artificially, severe infection was obtained, showing that these plants do not possess any inherent resistance. Since the infected leaves do not fall off, the disease persists throughout the winter and summer, although infection appears to take place only in the warm season. Inoculations made outdoors in November did not cause infection.

#### PATHOGENICITY

The disease was produced in its typical form by inoculating outdoors attached shoots of *Pittosporum* shrubs. Inoculations were made by the following methods: (1) spraying the leaves by means of a hand sprayer with a spore suspension in water, the spores being taken from naturally infected leaves; (2) transferring dry spores by means of a brush from naturally infected leaves to the undersurfaces of healthy leaves; (3) placing infected leaves next to healthy ones in such a way that their under surfaces were in contact; (4) spraying with a mycelial suspension in water of a pure culture of the fungus. Non-inoculated checks were also pro-

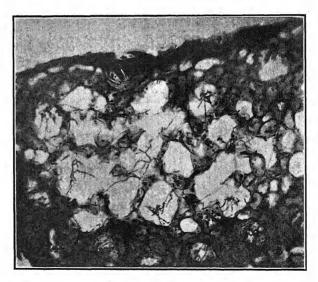


Fig. 2. Surface section of leaf showing profuse growth of mycelium beneath the lower epidermis with denser growth in the substomatal cavities.  $\times$  190.

vided. Some of the inoculated shoots in each series were placed under bell jars and some were left uncovered, but apparently covering the inoculated shoots with bell jars was unnecessary as the amount of infection on the covered shoots was not greater than on those left exposed. The inoculations were made between May and September when the atmospheric humidity was very high.

Results: Heavy infection was obtained in every case with methods 1 to 3, that is, when the inoculum consisted of spores from infected leaves. With pure culture inoculum, infection was very light (12 spots in one experiment and 7 in another). This was probably due to the fact that the cultures used as inoculum were not sporulating. Spots appeared on the inoculated leaves between 3 and 4 weeks after inoculation.

#### THE FUNGUS

The mycelium occurs both internally and externally. The internal mycelium occurs between both the palisade and the spongy parenchyma cells, but most profusely under the lower epidermis and especially in the sub-stomatal cavities where it forms a rather dense growth of interwoven hyphae. The hyphae in the sub-stomatal cavities which give rise to the sporophores do not become thickened, sclerotial, or tuberculate. The external mycelium arises either from the sub-stomatal hyphae, or as branches of the sporophores. In the young spots, the external mycelium is inconspicuous. In the older spots it forms, together with the sporophores and the entangled spores, a felty overgrowth which appears olive-brown in color, although the individual hyphae are hyaline.

The sporophores arise for the most part from the sub-stomatal hyphae of the internal mycelium, emerging in fascicles through the stomata of the lower epidermis (FIG. 3, A), though some may arise as branches of the external mycelium. They were never seen breaking through the epidermis. The young sporophores are practically hyaline, becoming only slightly dusky (never decidedly brown) with age. They are septate, alternately branched, procumbent,  $3.9-5.8\,\mu$  (ave.  $4.9\,\mu$ ) in diameter, and vary considerably in length (FIG. 4). It is difficult to determine accurately the length of the sporophores as some of the branches often elongate forming vegetative hyphae, and it is not always easy to tell where a sporophore ends and the vegetative mycelium begins. Fifty sporophores were measured and these varied in length from 22.0 to 65.0  $\mu$ , averaging 35.7  $\mu$ .

The conidia (Fig. 3, B) are long, slender, hyaline, septate, rarely constricted at the septa, cylindric to narrowly obclavate, straight or curved. They are mostly pointed at the base, and the points of attachment may be rounded or narrowly truncate. The length and degree of septation of the conidia vary with age (and probably with environmental conditions). One hundred spores from rela-

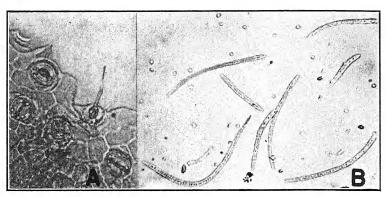


Fig. 3. A, free-hand section of lower epidermis showing conidiophores protruding through the stomata,  $\times$  230; B, conidia,  $\times$  350.

tively young spots, measured in May 1939, varied in size from  $34{\text -}109 \times 3.0{\text -}4.4~\mu$ , ave.  $72.0 \times 3.6~\mu$ , and in septa from  $3{\text -}12$ , ave. 5.8 per spore. A second lot of 100 spores from older spots varied in size from  $54{\text -}143 \times 3.4{\text -}4.4$ , ave.  $84.4 \times 3.7~\mu$ , and in septa from  $4{\text -}13$ , ave. 7.5 per spore.

The fungus was obtained in culture by tissue transfers and by isolating single conidia. It grows readily, although slowly, on a variety of media, producing olivaceous-gray to dark-gray colonies. Like many other members of this genus, it sporulates rather sparingly in culture. Some of the isolates sporulated more readily than others, but even the recalcitrant isolates were induced to sporulate by macerating the mycelium in sterile water and smearing the suspension on beanpod agar in plates. By this method, conidia were produced fairly abundantly.

#### TECHNICAL DESCRIPTION

#### Cercospora Pittospori sp. nov.

Spots angular, vein-limited, chlorotic, rarely necrotic, pale green to yellowish-brown above, light yellow to olive-brown below, solitary spots 1–5 mm., confluent spots much larger often covering more than one-half the area of the leaf. Mycelium internal and external, hyaline, regular to irregular, 2.0–4.4  $\mu$ ; external hyphae somewhat larger than the internal. Conidiophores hypophyllous, arising from the more or less loose sub-stomatal hyphae of the internal mycelium and emerging in fascicles through the stomata, or scattered on the external mycelium, procumbent, septate, hyaline to

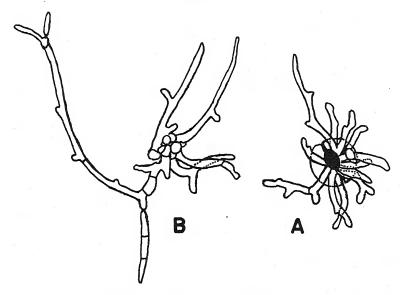


Fig. 4. Camera lucida line drawings of conidiophores of *Cercospora Pittospori*, × 578. A, relatively young conidiophores; B, older conidiophores considerably elongated.

slightly dusky (never decidedly brown),  $22-65 \times 3.9-5.8 \,\mu$ , alternately branched, some of the branches often elongating to form external mycelium. Conidia cylindrical to narrowly obclavate, straight or curved, narrowing at the base with their point of attachment rounded or narrowly truncate, hyaline,  $34-143 \times 3-4.4 \,\mu$ , 3-13 septate, occasionally constricted at the septa.

<sup>2</sup> Maculis angularibus, veno-limitatis, chloroticis, raro necroticis, supra e viridi pallentibus vel fulvis, infra luridis vel olivo-brunneis; maculis solitariis 1–5 mm., maculis confluis multo maioribus, areae folii partem dimidia maiorem obtendentibus; mycelio interiori atque exteriori, hyalino ad normam exacto vel abnormi, 2.0–4.40  $\mu$ ; hyphis exterioribus aliquanto amioribus quam interioribus; conidiophoris hypophyllis, e hyphis mycelii interioris hypostomaticis plus minusve laxis exsistentibus et in fasciculos per stomata emergentibus, vel in mycelio exteriori dissipatis, pronis, septis, hyalinis vel suffuscis (subnigris numquam), 22–65  $\times$  3.9–5.8  $\mu$ , ramis alternis, quorum quidam se producunt ut mycelia exteriora fiant; conidiis cylindratis vel subtiliter obclavatis, erectis vel curvatis, ad basim coartatis, coniunctione orbiculata vel truncata, hyalinis, 34–143  $\times$  3.0–4.4  $\mu$ , 3–13 septatis, ad septa interdum contractis.

On living leaves of Pittosporum tobira, Ait.

Type Locality: Baton Rouge, Louisiana.

Type specimens deposited in the herbarium of the Department of Botany, Louisiana State University, and also in the Mycological Collections, Bureau of Plant Industry, Washington, D. C.

DEPARTMENT OF BOTANY,

LOUISIANA AGRICULTURAL EXPERIMENT STATION,

UNIVERSITY, LOUISIANA

<sup>2</sup> The author is indebted to Dr. P. G. Moorhead, Professor of Latin, Louisiana State University, for assistance in writing the Latin diagnosis.

# MOLLISIA TETRICA, PEZIZA SEJOURNEI, AND THE GENERA PHAEOCIBORIA AND PYCNOPEZIZA

H. H. WHETZEL AND W. LAWRENCE WHITE

Von Höhnel (1918a), placing the customary emphasis upon spore color as a generic character, erected the genus Phaeociboria to provide for an inoperculate Discomycete having brown onecelled ascospores and a prosenchymatous medullary excipulum, yet not referable to Lambertella v. Höhn, nor to Velutaria Fuckel, the only other genera of the inoperculates known to him to have this combination of characters. His concept of the new genus was formed from a consideration of two species which he took to be identical. These two species had been described originally by Quélet (1885) and by Boudier (1881) as Mollisia tetrica and Peziza Sejournei respectively. Von Höhnel's only first hand knowledge of them appears to have been obtained from an examination of two specimens of M. tetrica, one distributed by Jaap in his Fungi Selecti Exsiccati No. 501 under the name Aleurina tetrica (Quél.) Rehm in litt., and the other by Rehm in his Ascomycetes Exsiccati No. 2153 as Humaria tetrica Quél. There is no evidence that von Höhnel had ever examined specimens of P. Sejournei Boud. Pending our suggestion of a generic resting place for each of these species later in this paper, we shall use their original designations in the following discussion of the problem.

Through his primary interest in *M. tetrica* von Höhnel was lead to a consideration of *P. Sejournei* largely because both species occur on *Hedera Helix*. After a comparison of the descriptions and the specimens of *M. tetrica* which he had before him, with the descriptions and illustrations of *P. Sejournei*, he concluded that the two are specifically identical notwithstanding his recognition of the following facts, viz.:

. (1) that the apothecia of M. tetrica are minute, about 1 mm. in diameter, and very dark in color; that they arise from areas in the

leaf parenchyma bordered by a black line, while the apothecia of *P. Sejournei* were described as 2–5 mm. in diameter, light in color, arising from petioles and midribs;

(2) that the ascospores of M. tetrica are fusiform to boatshaped, brown,  $20-22 \times 3.5-4.5 \,\mu$ , while those of P. Sejournei were described as ovoid oblong, sometimes a little curved, hyaline,  $11-13 \times 4-5 \,\mu$ .

His argument in support of his conclusion that the two are specifically identical is based upon his assumption that the size and shape of the ascospores vary greatly in both forms and that the ascospores of the specimens on which Boudier based his description of P. Sejournei were immature, hence small and uncolored. As a character indicating close relationship or identity of these two species, von Höhnel emphasizes the significance of peculiar colored structures which he observed in the hymenium of M. tetrica and similar structures reported by Boudier in P. Sejournei. His interpretation of these structures is without foundation in fact. A careful examination of these colored structures in M. tetrica shows them to be merely asci from which the more or less shrivelled ascospores have not been discharged. Boudier (Ic. Myc. pl. 484) pictures an ascus with undischarged spores and colored protoplasmic residue. The writers have been unable to find any appreciable number of such asci in the specimens of P. Sejournei which they have examined.

In the first of two notes on the matter (1918a) von Höhnel discusses a specimen from Rehm's Ascomycetes, No. 2153, distributed under the name Humaria tetrica Quél. [=Aleurina tetrica (Quél.) Rehm]. This collection on dead leaves of Hedera Helix, had been made by Jaap near Triglitz in Brandenburg in April, 1915. He first questions whether this material really represents a specimen of Quélet's Mollisia (Humaria) tetrica, and then assuming that it does, he further suggests that it may be identical with P. Sejournei Boud., citing Boudier's illustration of the latter species in Icones Mycologici, plate 484. Rehm's material appeared to him to be similar to Boudier's fungus in external characters, and like it occurring also on decaying leaves of the ivy. He notes that P. Sejournei "kürzere hyaline Sporen, während der ausgegebene Pilz längere, schliesslich rauchgraubraune Sporen hat."

He further points out that the Rehm specimen is inoperculate, having, like Lambertella v. Höhn. and Velutaria Fuckel, colored spores; that it is in structure a Ciboria; and that it, therefore, represents a new genus which he names Phaeociboria. He concludes his brief note with the remark, "Er hat Phaeociboria tetrica (Qu.) v. H. oder Phaeociboria Sejournei (Boud.) v. H. zu heissen, was noch zu entscheiden ist."

In his second more extensive note (1918b) entitled "Über Mollisia tetrica Quél.," evidently written but a short time after the first, von Höhnel repeats the information given in his earlier note, adds some new observations following his examination of an additional specimen of the fungus taken from the same locality five years later by Jaap (Fung. Sel. Exs., 501), and commits himself more completely to a belief in the specific identity of M. tetrica Quél. and P. Sejournei Boud. Since the specific name Sejournei (1881) has priority over tetrica (1885) he proposes in his concluding statement the combination *Phaeociboria Sejournei* (Boud.) v. Höhn. for the type species, saying, "Wenn beide Formen zusammengehören, muss der Pilz Phaeociboria Sejournei (Boud.) v. H. gennant werden, da Boudier den Pilz zuerst beschrieben hat, im anderen Falle tritt Ouélet's Artname in Kraft." Thus it is evident that in his final analysis von Höhnel was still uncertain as to the identity and affinities of Pesiza Sejournei Boud.

The writers were recently led to a consideration of this case by the thought that *P. Sejournei* Boud. might be a species of the genus *Pycnopeziza* which they had erected in 1938. Discussing this possibility shortly after the publication of the paper on *Pycnopeziza*, and with Boudier's colored illustration of *P. Sejournei* before him, the senior author recalled that he had collected a discomycete of similar aspect in May, 1930 in company with Dr. Eugene Mayor in the Perreux Forest near Neuchatel, Switzerland. Correspondence with Dr. Roger Heim of the Museum National d'Histoire Naturelle, Paris, disclosed the fact that while most of Boudier's herbarium is preserved in good condition at that institution, no specimen of *P. Sejournei* is to be found there. However, examination of the Neuchatel specimen and of the notes taken on the fresh material left no doubt in the writers' minds of its identity with *P. Sejournei* Boud. Although an ascospore cul-

ture from the specimen had been obtained at the time of its collection, this had died out, but a dried specimen of a petri dish culture on potato dextrose agar showing small flat black stromata had been preserved.

On January 11, 1939, a letter was addressed to Dr. Mayor asking him to make if possible another collection of *P. Sejournei* and to send it in fresh condition so that a pure culture of the fungus might again be obtained. Early in May, 1939 a fine collection of this fungus which he had taken on May 7 was received from Dr. Mayor. It was in good condition, but efforts to get cultures failed. However, the specimens provided excellent material for critical study. Failure to find in this material any traces of a conidial stage, which might confirm the "hunch" that *P. Sejournei* may be referable to *Pycnopeziza*, lead to the abandonment of that idea for the time being.

Meantime, the junior writer, scouting the literature and various herbaria for species which might be referable to the genus Rutstroemia Karst. emend. Rehm (1893) discovered that Ciboria pachyderma Rehm is identical with Pycnopesisa quisquiliaris (Ellis & Ev.) White & Whetzel. It is interesting in this connection that Rehm (1893) in his original description of Ciboria pachyderma says in a footnote: "Gehört zu Ciboria trotz kurz und dick gestielter Apothecien. Die auffällig kleinen Sporen trennen die Art von den bekannten; äusserlich nähert sie sich der Phialea Sejournei Boud. . . . deren Sporen 8-10 µ lang sind und zwei Oeltropfen enthalten." Later when Rehm (1915) transferred P. Sejournei Boud. to Ombrophila he listed Ciboria Sejournei Rehm as a synonym and cited his above quoted observation on the similarity of Ciboria pachyderma to that fungus. This seems to be the first and only place where the combination Ciboria Sejournei has been made and strongly suggests that Rehm thought his Ciboria pachyderma might be identical or at least congeneric with Boudier's species.

With this background of history, observation, and fact before the reader, it is now possible to give consideration to the question of the proper disposition of the species involved in the above discussion.

More fortunate than von Höhnel, the writers have had before

them for comparative study fairly satisfactory material of both Mollisia tetrica Quél. and Peziza Sejournei Boud. The junior author has examined critically specimens of the former from Jaap's Fungi Selecti Exsiccati No. 501 and from Rehm's Ascomycetes No. 2153, which are the collections seen by von Höhnel, and he has compared them very carefully with the excellent materials available of Peziza Sejournei Boud. This study confirms the accuracy of the original descriptions of the two species and fully establishes that they are specifically distinct. Not only are they distinct specifically, but they would seem best treated at the present time as different generically. It is therefore proposed that the genus Phaeociboria v. Höhn. be retained, with Mollisia tetrica Quél. as the type species, and that Peziza Sejournei Boud. be referred to the genus Pycnopeziza.

The validity of colored spores as a generic character in the Helotiaceae may be questioned. Several dark-spored species are at hand which do not appear to be closely related phylogenetically. The closest kin of each will probably be found among hyaline-spored forms. It seems probable in the light of present knowledge of these discomycetes that the brown-spored species may eventually be interpolated among, and considered congeneric with, certain hyaline-spored species to which on the basis of structural characters or on other grounds they would appear to be related.

There are certain structural features of *Mollisia tetrica Quél*. which are common to the species of the genus *Pycnopesiza* White & Whetzel. The genera *Phaeociboria* von Höhn. and *Pycnopesiza* White & Whetzel would therefore seem to be on the best evidence available at present, closely related and in turn allied to *Rutstroemia* Karst. emend. Rehm (type = *Pezisa firma* Pers.). A monograph of the latter genus containing some forty species is being prepared by the junior author, and will be ready for publication in the near future; the question of phylogeny and relationships will then be treated at greater length.

The following resumé of the genera *Phaeociboria* and *Pycno-peziza* is presented.

Phaeociboria von Höhnel, Ann. Myc. 16: 220. 1918.

Since von Höhnel did not give a formal generic diagnosis the writers present the following:

Apothecia small, stipitate or substipitate, brown or brownish; disc expanded, finally convex, of medium thickness, waxy-cartilaginous when dry; margin circular, obtuse, smooth; receptacle smooth; context light ochraceous brown; in section, differentiated into a thin faintly yellowish hypothecium, a broad colorless medulary layer of loosely interwoven, hyaline, thin-walled hyphae, and a nearly colorless ectal layer of rather compact, parallel, thin-walled hyphae radiating from stipe to margin; paraphyses simple, filiform, colorless; asci clavate-cylindric, opening by a pore; spores narrowfusoid, brown, one-celled. Type species: *Mollisia tetrica* Quél.

It has not been possible to determine the exact dates of publication of von Höhnel's two notes on Mollisia tetrica, in each of which with an equal show of validity he proposes the generic name Phaeociboria. Contrary to previous practice 1 by which Fragmente zur Mykologie No. 1123 (1918b) is cited as the place of first publication of the genus Phaeociboria, the writers have designated the briefer note in Annales Mycologici (1918a) because it very evidently was the first article written. In neither article was a formal generic diagnosis presented, and in each of them Peziza Sejournei and Mollisia tetrica were assumed to be identical. Yet it is clear from the context of either note that the genus was founded primarily on the characters of M. tetrica; that mention of P. Sejournei in this connection was merely incidental; and that the latter species, in so far as von Höhnel was concerned, is to be disregarded should future investigation prove it a distinct species. Hence, recognition of the genus Phaeociboria is not open to criticism on the ground that it was founded on error.

Phaeociboria tetrica (Quél.) von Höhnel, Ann. Myc. 16: 220. 1918.

Mollisia tetrica Quél., Assoc. Fr. Av. Sci. Compte Rendu 14<sup>2</sup>: 452. 1886.

Humaria tetrica Quél. Ench. Fung. 291. 1886. Velutaria tetrica Rehm, Rab. Krypt.-Fl. 1<sup>3</sup>: 647. 1893.

<sup>&</sup>lt;sup>1</sup> Clements & Shear, 1931, p. 327; Kanouse, 1935, p. 75; Nannfeldt, 1932, p. 298.

Aleurina tetrica Rehm, Verh. Bot. Ver. Prov. Brand. 56: 77. 1914.

Apothecia solitary, small, substipitate, appearing sessile, attached by a papilla-like central projection, 1–1.5 mm. in diameter; when dry, medium brown to nearly black, more or less concolorous throughout, waxy-cartilaginous, plane to slightly convex; when moistened becoming strongly convex, medium brown, ceraceouscoriaceous, the margin obtuse; in section the hymenium 95–105  $\mu$ thick, conspicuous on account of the numerous brown spores in the asci; hypothecium about  $40 \mu$  thick, prosenchymatous, pale brownish to nearly colorless, the hyphae compactly interwoven,  $3-4.5 \mu$  in diam.; medullary layer broad, hyaline, composed of branching, rather loosely interwoven, septate, thin-walled hyphae,  $6-7 \mu$  in diam.; ectal layer not well differentiated, colorless to very slightly brownish, composed of rather compact longitudinally interwoven, thin-walled, short celled hyphae of about the same diameter as those of the medullary layer, not protruding at margin beyond the hymenium; paraphyses simple, colorless, slightly clavate toward the apex,  $3-3.5 \mu$  in diam.; asci clavate cylindric 100- $110 \times 10$ – $12 \mu$ ; spores one-celled, biseriate, at first hyaline, narrowly fusoid with 4-6 irregular oil globules, soon becoming cinnamon brown, narrow oblong-fusoid, slightly inaequilateral, 18- $24 \times 4-5.5 \mu$ , the ends obtuse.

Habitat: On *Hedera Helix*; reported on dead stems and leaves; noted by the writers only on the leaves, arising directly from the leaf blade, unassociated with the veins.

Type locality: Vosges, France.

DISTRIBUTION: Known only from France and Germany. Apparently rare. "Autonine" (Quélet), April.

France: Vosges (Original description of Quélet).

Germany: Triglitz (Prignitz), Prov. Brandenburg, April 15, 1911; <sup>2</sup> a second collection from same locality, col. Jaap, April, 1915, Rehm, Ascom. Exs. 2153.<sup>3</sup>

Illustrations: Quélet, Assoc. Fr. 1885, pt. 2, pl. 12, f. 27. 1886.

Exsiccati: Jaap, Fung. Sel. Exs. 501; Rehm, Ascom. Exs. 2153.

<sup>&</sup>lt;sup>2</sup> Specimen examined, from Fairman Herb. in Dept. Plant Pathology, Cornell University.

<sup>&</sup>lt;sup>3</sup> Specimens examined, from Farlow Herb. (no apothecia found), and from U. S. D. A., Path. & Mycol. Collections (one apothecium present).

Pycnopeziza White & Whetzel, Mycologia 30: 187. 1938.

This genus was founded to include species having certain distinctive apothecial characters and a highly characteristic conidial stage. An adequate generic diagnosis was presented in the previous paper (White & Whetzel, 1938) and need not be repeated here. Type species: *P. sympodialis* (Bub. & Vleug.) White & Whetzel.

Pycnopeziza Sejournei (Boud.) comb. nov.

Peziza Sejournei Boud. Bull. Soc. Bot. France 28: 94. 1881. Phialea Sejournei Boud. Icon. Myc. 4: 282. 1905–1910. Ciboria Sejournei Rehm, Ber. Bayer. Bot. Ges. 15: 246. 1915. Ombrophila Sejournei Rehm, Ber. Bayer, Bot. Ges. 15: 246. 1915.

Phaeociboria Sejournei von Höhnel, Ann. Myc. 16: 220. 1918.

Apothecia solitary, substipitate, erumpent, at first turbinate, reaching a diameter of 2-6 mm., thick, fleshy; externally pale ochraceous brown, furfuraceous; stipe short, thick, often scarcely distinct, broadened rather gradually above into the receptacle; margin circular, obtuse; hymenium patelliform, finally plane or slightly convex, yellowish- or reddish-brown in color; in drying changing color and shape but little, the hymenium becoming very dark reddish brown and slightly concave, the stipe-like basal portion rather deeply lacunose-wrinkled, when broken showing a thick pale brown or deep cream color and a more or less powdery context. In section showing a narrow, yellowish, poorly defined hypothecium about 30 \mu thick, composed of narrow compactly interwoven hyphae; medullary excipulum broad, colorless, homogenous, the hyphae rather compactly interwoven, thin-walled, 4-7  $\mu$  in diam.; ectal layer not well defined, faintly yellowish, composed of compactly and longitudinally interwoven hyphae which on the outer surface and especially toward the stipe are broken into thinwalled isodiametric cells,  $10-15 \mu$  in diameter. Paraphyses simple, scarcely or not at all enlarged above, colorless, 3.5-4.5 u in diameter; asci cylindric above, narrowed below, 95–110  $\times$  7.5–8.5  $\mu$ ; spores hyaline, 1-celled, sometimes with a small oil globule in each end, narrow ellipsoid,  $9-13 \times 4.5-5 \mu$ , obliquely or more or less irregularly uniseriate.

HABITAT: On *Hedera Helix*; dead stems, petioles, and basal portions of leaf veins.

Type locality: Blois Forest, France.

DISTRIBUTION: Known only from central Europe. Evidently not common. April and May.

France: Blois Forest (Original description of Boudier), May; Presle, April 23, 1910 (Specimen examined from Patouillard Herb. in Farlow Herb., Harvard Univ.).

Germany: Aschaffenburg. Report by Rehm (1915, p. 246) based on a collection by A. Ade. Von Höhnel suggests that Rehm's specimen may be incorrectly named.

Switzerland: Neuchatel, Perreux Forest, May 11, 1930, H. H. Whetzel, Cornell Univ. Pl. Path. Herb., 27980; Perreux Forest, May 7, 1939, E. Mayor, Cornell Pl. Path. Herb., 28442.

Illustrations: Boud., Bull. Soc. Bot. Fr. p. 94, pl. 2, f. 4, 1881; Boud., Icon. Myc. 3: pl. 484, 1905–10.

While no conidial stage has been found in the material available for examination, the characteristic apothecial features nevertheless seem to indicate a close relationship with the species previously discussed by the writers (1938) as *Pycnopeziza quisquiliaris*, and for which a new combination must now be proposed (see below). From the latter it differs only in having slightly larger spores, a considerably thicker medullary excipulum, thicker stipe, and in its occurrence on *Hedera Helix*. The writers had hoped for the discovery of a conidial stage corresponding to those of the species previously included in *Pycnopeziza* which would of course have fully confirmed the proposed disposition of this very interesting species.

## Pycnopeziza pachyderma (Rehm) comb. nov.

Ciboria pachyderma Rehm, Rab. Krypt.-Fl. 1<sup>8</sup>: 758. 1893. Cyathicula quisquiliaris Ellis & Ev. Proc. Acad. Phila. 1893: 451. 1894.

Pycnopeziza quisquiliaris White & Whetzel, Mycologia 30: 192. 1938.

The new combination is necessitated by the discovery of the fact that Ciboria pachyderma Rehm is synonymous with Cyathicula quisquiliaris Ellis & Ev. and has priority over the latter by one year. Under the name Ciboria pachyderma the species has been distributed in Sydow's Mycotheca Marchica as Nos. 1269, 3480,

3777, 3955, and 4157, and in Rehm's Ascomycetes as No. 758; all of these were taken in Germany. Examination of these specimens together with reports of the species under the same name by Rehm (1893, p. 758), Dodge (1914, p. 1033), and Velenovský (1934, 1:217; 2: pl. 22, f. 11) calls for no modification of the description already presented (White & Whetzel, 1938). However, certain data concerning distribution, substrata, etc. may be briefly summarized. The species is now known in North America from Iowa, New York, West Virginia, and Wisconsin, and in Europe from Czechoslovakia and Germany. The substrata include decaying leaves of Alnus rugosa, Prunus serotina, Quercus, Salix, and Spiraea, buds of Acer rubrum, and leaves of undetermined species (numerous collections). All of the North American and most of the European collections were made during the spring months of April, May, and June; exceptions are Sydow, Mycotheca Marchica Nos. 3480, 3955, and 3777 taken in Sept., Oct., and Nov. respectively. Specimens of these were examined at the New York Botanical Garden more than a year ago and are not at hand now for reexamination. It is possible that they represent minor variations of the species, for in the experience of the writers most species of the Ciborioideae have a restricted seasonal period of apothecial production.

Pycnopeziza pachyderma var. depressa Vel. Monogr. Discom. Boh. 1: 217. 1934.

"Apoth. sublobata, ochracea, centro infundibuliformi-impressa, stipite concolor. Ad folia quercina in valle prope Zahorany maio 1927 leg. Cejp."

The above description by Velenovský, though entirely inadequate for certain recognition of the form, is strongly suggestive of *Pycnopeziza sympodialis*. However, until Velenovský's specimen can be critically examined it seems best to leave it where the author originally placed it.

Pycnopeziza sympodialis (Bub. & Vleug.) White & Whetzel, Mycologia 30: 190. 1938.

Acarosporium sympodiale Bub. & Vleug., Ber. Deutsch. Bot. Ges. 29: 385. 1911.

In the previous publication by the writers, three types of fruiting

structures were described as occurring in the life cycle of P. symbodialis. Only North American material was then at hand. The conidial fungus Acarosporium sympodiale, known only from the type collection taken in Sweden, was assumed to represent the conidial stage of this pleomorphic species, and this with little misgiving since the characterization by Bubák (1911) of this very distinctive form was wholly adequate. When it was learned recently that the Bubák Herbarium is now at the Brooklyn Botanic Garden, and not in Europe as the writers had formerly assumed, the type specimen was borrowed for study. Only the conidial stage is present in the small amount of leaf debris in the type packet. The pycnidia are fairly numerous and are in excellent condition. Agreement of the pycnidial stage from the North American material with this European type is so wholly complete as to remove all doubt of their specific identity. A second collection in the Bubák Herbarium which bears the same data as the type, except that it was taken a year later, is rather unsatisfactory for study, but enough of the conidial stage was found to make identification with the type positive.

The writers wish to express their thanks to Professor H. M. Fitzpatrick for critical reading of the manuscript; to Dr. D. H. Linder, Farlow Herbarium, Harvard University, Dr. G. M. Reed, Brooklyn Botanic Garden, Dr. F. J. Seaver, New York Botanical Garden, and Mr. John A. Stevenson, U. S. Dept. of Agriculture, for making available for examination specimens from their respective herbaria; to Dr. Roger Heim of the Paris Museum for information concerning Boudier collections of *Pycnopeziza Sejournei*; and to Dr. E. Mayor of Neuchatel, Switzerland, to whom they are especially indebted for furnishing fresh material of *P. Sejournei*.

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## A FURTHER REPORT ON THE UREDI-NALES OF COLOMBIA <sup>1</sup>

FRANK D. KERN AND H. W. THURSTON, JR.

Several comprehensive accounts of the rust-flora of Colombia have been published. The first was a most excellent paper by Dr. Eug. Mayor in 1913 entitled "Contribution à l'étude des Uredinées de Colombie" (Mem. Soc. Neuch. Sci. Nat. 5: 442–599). This paper was well illustrated and in it the author set forth the character and standing of the rust species with clarity and exactness. It has been the foundation for all subsequent studies of Colombian rusts. Not only that, it has been invaluable in all investigations of West Indian and South American Uredinales.

During the years 1926–29 Messrs. C. E. Chardon, J. A. B. Nolla, and R. A. Toro made extensive collections of fungi in Colombia. The rust specimens were placed in the hands of F. D. Kern and H. H. Whetzel. As a result of their studies a section on Uredinales was contributed by them in 1930 to "Mycological Explorations of Colombia" (Jour. Dept. Agric. Puerto Rico 14: 301–348).

Three years later Kern, Thurston, and Whetzel published an "Annotated Index of the Rusts of Colombia" (Mycologia 25: 448–503). In this paper an attempt was made to include all of the species of rusts known to occur in the country. This 1933 list presented many changes and additions when compared with the 1930 list. In explanation the following statement was made: "Changes may be due to the discovery of additional spore-forms, or they may be due to additional characters discoverable from the specimens but not from the descriptions, or to mistaken identity of hosts, or to some combination of these or other new data."

<sup>&</sup>lt;sup>1</sup> Contribution from the Department of Botany, The Pennsylvania State College, No. 131. Publication authorized on February 24, 1940 as paper No. 958 in the Journal Series of the Pennsylvania Agricultural Experiment Station.

Again we have changes and additions. There are several changes in names which seem necessary. We are abandoning the name Puccinia epiphylla and taking up Puccinia Poae-sudeticae as explained in the note. The Geranium rust has become Puccinia unilateralis. As a result of the discovery of teliospores it has been taken from the form-genus Uredo. In the 1930 paper an aecium on Capsicum was described as Aecidium Capsici. Teliospores have been found which complete the life cycle. Since there is a microcyclic Puccinia under the specific name Capsici a new name must be provided. We are proposing Puccinia capsicicola. merous collections of rust on species of the genus *Inga* have been made in Colombia. The 1930 and 1933 papers referred all collections to Ravenelia Ingae. The most recent opinion is that two species are present—one to be called Bitzea Ingae and the other Uredo Ingae. Uredo jatrophicola now becomes Phakopsora jatrophicola through the discovery of teliospores.

Although not much mycological exploration has been carried out in Colombia since 1933 we have had for study approximately fifty specimens. These have been collected chiefly by Dr. Carlos E. Chardon. We are now reporting that eleven species are added to the number reported in 1933, bringing the total up to 226. Two of these are described as new. One species was added in 1939 by the description of the new genus *Chardoniella* (Kern, Mycologia 31: 375). Another species appears because of the separation of *Ravenelia Ingae* into two species. This means that seven species are now recognized for the first time from Colombia owing to the collections of Chardon in 1936 and in 1937. Two of these have not been reported previously from South America.

AECIDIUM CAPSICI Kern & Whetzel. See *Puccinia capsicicola*.

Bitzea Ingae (Sydow) Mains, Mycologia 31: 38. 1939. Maravalia Ingae Sydow, Mycologia 17: 257. 1925.

In the 1933 paper nine collections were referred to Ravenelia Ingae. Of these the following are now regarded as belonging to the species Bitzea Ingae:

On Inga adenophylla Pittier, Toro 190.

Inga edulis Mart., Chardon 110. Inga cf. ingoides (Rich.) Willd., Mayor 311. Inga spuria H. & B., Archer H-34. Inga sp., Chardon & Nolla 448; Chardon 90.

These specimens all have present one-celled spores with markings consisting of prominent longitudinal ridges and less pronounced cross ridges. This spore-form has been described twice in the genus *Uromyces* as telia (*U. ingicola P. Henn. and U. porcencis Mayor*) and once in the genus *Ravenelia* as uredinia (*Ravenelia Whetzelii Arth.*). Without doubt these striately marked spores are urediniospores and according to Mains they are a part of a life cycle of his species *Bitzea Ingae*.

There is present in Colombia a spore-form on *Inga* with echinulate markings. According to Mains this form "may possibly be the secondary uredinia of *Bitzea Ingae* but the evidence appears to be against it." We are following Mains in listing collections of this sort under *Uredo Ingae*.

CHARDONIELLA GYNOXIDIS Kern, Mycologia 31: 375. 1939. On *Gynoxis* sp., Cerro Monserrate pr. Bogotá, alt. 2750 m., March 12, 1937, C. E. Chardon 829.

Known only from the type specimen.

Mainsia cundinamarcensis (Mayor) Jackson, Mycologia 23: 114. 1931.

On Rubus sp., Peña negra, above Facatativa, March 28, 1937, C. E. Chardon 856.

Our specimen agrees so well with Mayor's original collection that we have no hesitation in referring it to this species. Jackson has called attention to the fact that the urediniospore wall is distinctly thickened at the apex although this was not mentioned by Mayor. Jackson said the markings are much more prominent at the apex than at the base. We think he should have added that the apical markings are of a ridge-like nature giving the effect of striations. The species is known also from Venezuela and Ecuador.

Phakopsora columbiana Kern & Whetzel. Jour. Dept. Agric. Puerto Rico 14: 304. 1930.

On Croton gossypiifolius Vahl, Girmania, Viteletes, alt. 1025 m., April 11, 1937, C. E. Chardon 861.

This species was described from Ibagué, Colombia, where it was collected by C. E. Chardon, June 20, 1929, no. 555. The original description states that the urediniospores are  $23-27\times26-31~\mu$ , the walls cinnamon brown, echinulate,  $2~\mu$  or more thick. That description does not cover the range of these spores. A restudy reveals many spores of large size,  $24-32\times29-42~\mu$ , with walls from  $3-6~\mu$  thick, yellowish, and strongly aculeate. It is possible that these lighter thicker walled spores are immature. Dr. G. B. Cummins has recently sent us a specimen from Trinidad, said to be on the type-host, *Croton gossypiifolius* Vahl, which agrees perfectly with the type as regards the urediniospores.

Phakopsora Jatrophicola (Arth.) Cummins, Bull. Torrey Club 64: 43. 1937.

Specimens previously cited under *Uredo jatrophicola* are now referred to the genus *Phakopsora*. Dr. Cummins found telia on a specimen from Lower California. He says the rust is common in tropical North America. It is known also from Colombia, Brazil, and Venezuela in South America.

Puccinia Anthephorae (Sydow) Arth. & Johnston, Mem. Torrey Club 17: 137. 1918.

On Anthephora hermaphrodita (L.) Kuntze, Finca Santander, Cucuta, December 7, 1936, C. E. Chardon 815.

This species has heretofore been known only from the West Indies. Arthur and Johnston commented that it "is doubtless widespread, although it may not be abundant, throughout the West Indies, as the host is a wayside weed." It is interesting that no other collections have turned up from the West Indies and this is, so far as we know, the only additional report of the species.

Puccinia capsicicola nom. nov.

Aecidium Capsici Kern & Whetzel, Jour. Dept. Agric. Puerto Rico 14: 341. 1930.

Not Puccinia Capsici Mayor, Mem. Soc. Neuch. Sci. Nat. 5: 501. 1913.

A reexamination of the type specimen has revealed the presence of a few telia. They arise in the old aecial cups in such a way that there can be no question of their relationship. The species is therefore a *Puccinia* of the opsis-type. We would describe the telial stage as follows:

Telia in the old aecia, blackish; teliospores broadly ellipsoid.  $18-23 \times 37-55~\mu$ , rounded above and below, slightly constricted at the septum, the wall chestnut-brown, smooth,  $3-4~\mu$  thick, slightly thicker at apex,  $5-6~\mu$ ; pedicel short.

This species is similar to *Puccinia paulensis* Rangel (Archiv. Jard. Bot. Rio de Janeiro 2: 70. 1918) but differs in having teliospores that are narrower and longer and aeciospores that are smaller and thicker walled.

Puccinia epiphylla (L.) Wettst.

See Puccinia Poae-sudeticae (Westend.) Jørstad.

Puccinia Gnaphalii (Speg.) P. Henn. Hedwigia Beibl. 41: 66. 1902.

On Gnaphalium spicatum Lam., LaVirginia, camino del Ruiz, alt. 2700 m., December 25, 1936, C. E. Chardon 839.

This species is known from the Southern United States, Central America, and several South American countries but we have found no previous report from Colombia.

Puccinia Heliotropii Kern & Kellerm. Jour. Myc. 13: 23. 1907.

On Heliotropium indicus L., Finca Santander, Cucuta, December 7, 1936, C. E. Chardon 814.

The first report of this species from Colombia. It is otherwise known from Guatemala and Venezuela. We know of a total of only five collections from all localities.

### Puccinia immensispora sp. nov.

Pycnidiis epiphyllis, paucis, in maculis decoloratis teliis objectis, profunde insidentibus, conspicuis, punctiformibus, magnis, usque 300  $\mu$  diam., periphysibus brevibus.

Teleutosoris hypophyllis, gregariis vel confluentibus, in greges circinatim dispositis 2–3 mm. diam., nudis, ceraceis, dein ob germinationem pulverulentibus, flavis; teleutosporis oblongis vel anguste oblongo-ellipsoideis, 31–40  $\times$  125–170  $\mu$ , supra rotundatis vel angustatis, infra angustatis, ad septum leniter constrictis; tunica hyalina vel tincta, 3–5  $\mu$  cr., leve; pedicello lato, sporam aequante vel breviore.

On Diplostephium sp. (?), paramo de Chipaque, alt. 1000 m., April 1, 1937, C. E. Chardon, E. Perez Arbelarz, H. Garcia Barrios 840.

The outstanding characteristic of this species is the large size of the teliospores. Sydow in his Monographia Uredinearum, vol. 1, p. 190, said that Puccinia nervincola Lagerh. from Ecuador had the largest teliospores of all the species of Puccinia. The size given for that species is  $14-22 \times 135-162 \,\mu$ . Our species has spores that are much broader and there are other differences such as the apical thickness of the walls. Sydow has recently described two other species of Puccinia with large spores, both from Ecuador. Neither of them equal our species in size of the spores and there are other differences as well.

All of Sydow's species are on undetermined hosts. Our specimen is not without some doubt. Dr. S. F. Blake has said that it is probably *Diplostephium*.

## Puccinia liabicola sp. nov.

Pycnidiis epiphyllis, paucis, gregariis in maculis decoloratis, 2–3 mm. diam., profunde insidentibus, obscure bruneis, conspicuis, subepidermalibus, globoidiis  $175-190~\mu$  diam., periphysibus brevibus.

Teleutosoris hypophyllis, in maculis dense aggregatis et pycnidiis objectis, mox nudis, rotundatis, cinnamomeo-brunneis ob germinationem cinerascentibus, 0.3-0.4 mm. diam.; epidermide rupta inconspicua; teleutosporis oblongis vel oblongo-clavatis, infra angustatis, supra rotundatis, leniter constrictis,  $23-27 \times 60-85 \,\mu$ ; tunica tenui ca.  $1\,\mu$ , hyalina vel tincta, leve; pedicello hyalino, lato, sporam dimidiam aequante.

On Liabum sp., Tequendama, December 13, 1936, C. E. Chardon 818.

A microcyclic species, resembling Puccinia Liabi in some ways,

but differing in the presence of pycnia and in certain well defined spore characters. In *Puccinia Liabi* the spores are brownish and  $14-21 \times 40-59 \ \mu$ . Here they are colorless, or slightly tinted, and  $23-27 \times 60-85 \ \mu$ . In the former the apical wall is thickened up to  $4 \ \mu$ , here the wall is uniformly thin.

Puccinia oblongula Jackson & Holw. Mycologia 18: 145. 1926.

On Rynchospora sp., Tequendama, December 13, 1936, C. E. Chardon 824.

There are present only urediniospores. They agree so well with the type that we have no hesitation in making this determination. This appears to be the first report outside the type locality which is in Ecuador.

Puccinia Poae-sudeticae (Westend.) Jørstad, Mag. Naturv. 70: 325. 1932.

On Poa annua L., gardens at El Colegio, near Madrid, March 29, 1937, C. E. Chardon 850.

Alopecurus aequalis Sobol., gardens at El Colegio, near Madrid, March 28, 1937, C. E. Chardon 858.

In our previous report (Mycologia 25: 469, 1933) we pointed out that the name Puccinia Poae-sudeticae seemed to be the proper name for this species but actually we used instead the name Puccina epiphylla. We are now convinced that the latter name refers to a northern species which does not occur in this region at all. It has no or very inconspicuous paraphyses in the uredosori. All of our specimens from Colombia have paraphyses and belong to Puccinia Poae-sudeticae. Besides the two specimens here referred to, there are also Chardon's numbers 616, 628, and 631, and Toro's number 410. We should add that many others have used the name Puccinia Poarum for this species but that is to be regarded as an erroneous use of the name. Puccinia Poarum Nielson is synonymous with Puccinia epiphylla (L.) Wettst.

Puccinia Polymniae Jackson & Holw. Mycologia 24: 167. 1932.

On Polymnia pyramidalis Triana, ravine between Monserrate and Guadalupe, above Bogotá, March 12, 1937, C. E. Chardon 825.

This is a species with an unusual form of urediniospores. They are vertically flattened with four subequatorial pores. It has been previously reported from Ecuador and Bolivia.

Puccinia unilateralis (Arth.) Cummins, Bull. Torrey Club. 67: 67. 1940.

On Geranium caucense R. Knuth, La Virginia, camino del Ruiz, alt. 2700 m., December 26, 1936, C. E. Chardon 811.

In a recent paper Cummins has transferred *Uredo unilateralis* to *Puccinia*. He found 2-celled teliospores on a specimen from Mexico. The teliospores are peculiar in that they are sessile on a cellular hymenium. In an earlier paper (Kern & Whetzel, Jour. Dept. Agric. Puerto Rico 14: 347, 1930) we reported *Uredo unilateralis* on *Geranium hirtum* from Colombia (*Chardon 596*). Teliospores have been found on this specimen and although they differ from the Mexican specimen in being narrower and in having a thinner apical wall Cummins expresses the opinion that this specimen probably belongs to the same species. The pycnia, aecia, and uredinia agree.

RAVENELIA INGAE (P. Henn.) Arth. See Bitzea Ingae (Sydow) Mains. Uredo Ingae P. Henn.

UREDO INGAE P. Henn., Hedwigia Beibl. 38: 69. 1899. On Inga sp., Chardon & Nolla 437, 490; Archer H-155. See note under Bitzea Ingae.

Uredo Jatrophicola Arth.
See *Phakopsora jatrophicola* (Arth.) Cummins.

Uredo Nidularii P. Henn. Hedwigia Beibl. 37: 206. 1898.

On Guzmania sp., ravine between Monserrate and Bogotá, March 12, 1937, C. E. Chardon 832.

Hennings described this species on *Nidularium* from Brazil. A specimen was issued in Rab. Fungi Eur. 4340. Through the kindness of Dr. D. H. Linder, of the Farlow Herbarium, we have had

the Rabenhorst specimen for comparison. Our specimen agrees well.

UREDO TRINIOCHLOAE Arth. & Holw. Am. Jour. Bot. 5: 538, 1918.

On Triniochloa stipoides (H. B. K.) Hitchc., hills about Facatativa, March 28, 1937, C. E. Chardon 854.

This species was described from Guatemala where it was collected in 1915. This is, so far as we know, the second collection.

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# "MUTATIONS" IN ASPERGILLUS NIGER BOMBARDED BY LOW VOLTAGE CATHODE RAYS 1

ROY M. WHELDEN (WITH 4 FIGURES)

The study of variations or of true mutations in organisms exposed to various forms of ionizing radiation has been carried forward actively ever since suitable sources of these various radiations were developed. Ultraviolet light, X-rays, high velocity cathode rays, radium, and neutrons have all been used more or less extensively. The greater number of variations that has been recorded, however, have occurred in higher animals and plants. Fungi have received relatively little attention. Nadson and Phillipov (7) have reported mutations in Mucor genevensis under X-ray exposure. The same authors (8, 9) later recorded the occurrence of permanent modifications in X-rayed yeasts. Other workers, notably Holweck and Lacassagne (6) and Nadson and Rochlin (6) abroad and Wyckoff and Rivers (12), in this country, have investigated modifications in yeasts exposed to ionizing radiations. Work on modifications in Aspergillus niger following the exposure of spores to high voltage cathode rays has been done by Haskins and Moore (5). Dodge (3) noted that X-raying ascospores in Neurospora tetrasperma has lethal effects. Dickson (2) showed that ultraviolet light, X-rays, and heat could produce saltations in Chaetomium cochliodes and other fungi, the saltants being distinguished from the parent strains by color differences, by changes in number and size of perithecia, or complete lack thereof. Quite recently Emmons and Hollaender (4) reported that dermatophyte spores exposed to ultraviolet light gave rise to several mutations.

It is the purpose of the present paper to describe a series of <sup>1</sup> Contribution from the Haskins Laboratories and from the Laboratories of Cryptogamic Botany and the Farlow Herbarium, Harvard University, No. 183.

variations occurring in plants of Aspergillus niger arising from spores subjected to conditions to which fungus spores have not been previously submitted; namely, bombardment in vacuum by low-density beams of low-velocity electrons, comparable in their density and range to the secondary electrons released in spore tissues under X-ray bombardment. The velocity of these electrons was so adjusted that the maximum ionization occurred in the region of the spherical, centrally located nucleus of the spore.

This work grew out of a three year study of the inactivation effects of low velocity cathode rays upon spores of Aspergillus niger in vacuum. Dry spores of the organism were spread, in a single uniformly distributed layer, one spore deep, on highly polished chromium-plated brass slides and mounted on a drum within the raying box of a cathode ray tube. The tube was sealed and evacuated, and the spores exposed to the electron beam under carefully controlled conditions, so that both velocity of electrons and total incident dosage to the spore-bearing plate were accurately known. The tube was then returned to atmospheric pressure, and the spores "printed" off into Petri dishes of potato-maltose agar and cultured and studied under standard conditions. This work has been described elsewhere (1). Except in those cases in which irradiation resulted in the death of every spore, single spore cultures were made for further study of as many of the irradiated spores as possible after each "run." In the early work very low speed electrons were used, of insufficient velocity to penetrate to the spore nucleus, or, in some cases, of sufficiently great velocity so that the ionization tracks ended well beyond it. The maximum ion concentration therefore lay in the cytoplasm. Among all the cultures studied from irradiations of this type, only one variation appeared, distinguished by its brown spores (11). Cultures of many successive generations of this variant have been made, without any apparent alteration.

When examination was begun of plants of Aspergillus arising from spores bombarded by electrons of 11.52 electron kilovolts energy, it at once became apparent that this voltage range was a rather critical one in the production of variations. Effects occurred here which were recognizable very early in the development of the spores. At all lower voltages the spores which had been

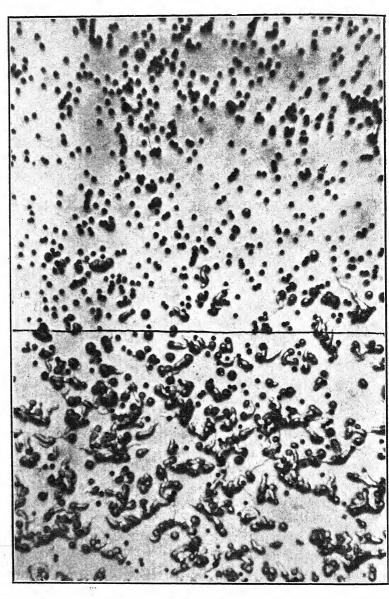


Fig. 1.

irradiated could be positively identified as "living" or "dead" at the end of approximately eight hours. "Living" spores were considered to be those which developed distinct germ tubes, well advanced at the end of the eight hour period. The obvious difference observable between "living" and "dead" spores at certain voltages and dosages is indicated in figure 1, which shows the appearance of spores on each side of the edge of the rayed band under heavy dosage and fairly low voltage.

It was found that when electron beams in the vicinity of 12 kv. were used, the clear-cut distinction between "living" and "dead" spores vanished. Under a calculated dosage of  $9.17 \times 10^{-5}$  ergs per spore at this voltage, there were obtained all degrees of germination, from spores showing germ tubes as far advanced as those of the controls to spores showing only the very slightest swelling at the end of the culture period. The determination of the 50 per cent survival ratio point was exceedingly difficult with these markedly indefinite or transitional spore effects. The wide range of stages of development between the active and the inactive condition is well shown in figure 2, where the controls are at the left half of the photograph, and the spores irradiated under the conditions described are at the right.

Another anomaly in cultures grown from spores irradiated under these conditions became apparent later in their development. As in all previous cases, the irradiated spores were transferred from the original culture to new agar plates for further study. At first single spore transfers were made, but later groups of 15 to 20 spores were transferred to the new agar surface. Similar transfers of control spores were made at the same time. A small transfer chamber was used throughout, sterilized as thoroughly as possible by steaming and washing all surfaces used with a solution of bichloride of mercury. After transfer, the dishes were set aside to permit development of the cultures until sporulation was well advanced. Since the survival ratio of the material was something under 50 per cent, not more than 10 of the 15–20 spores so transferred ordinarily developed.

After the cultures had "matured" so that spore formation was actively in progress, many showed "sector" formation (FIG. 3). Since not one of the control dishes showed such sector formation.

it seemed reasonable to attribute this result to irradiation. It also seemed logical to assume that each of these modified "sectors" arose from a single spore.

As soon as spores appeared in the modified sectors, subcultures were made from spores of each sector, and also from bits of mycelium from the edges of the cultures. These subcultures were grown until spore formation was well advanced when the process was repeated. In all, eight successive transfers were made from each of the original sectors. When the eighth transfer was made, one was also made from a spore of the original sector culture. The two resulting cultures were carefully compared, to check further variations which might have occurred after subculturing was begun. In all cases here reported no evident differences could be observed. It seems permissible to assume, therefore, that variation is fixed.

Specimens of each of the variants obtained in these early radiation runs were preserved in sealed tubes, all the others being destroyed when the eighth transfer had matured. Several weeks later the earlier work was carefully repeated. Four distinct variants had been obtained from the first run. The next run gave ten variant sectors. Certain of these presented features which made special treatment necessary. Two of these will be mentioned later. The third run gave four variants. The fourth run, from which over two hundred single spore transfers were made, gave five variants, two of which failed to survive transfers. One of the permanent variants, appearing in this run for the first time, was very noticeable because of its coarseness. Two later runs each gave about the same numbers of variants. At the end of the fifth run it was apparent that some of the variants of each run were quite like those of previous runs.

Comparative examinations show that most of the variants are referable to five distinct types. One of these types when its spores are fully mature, has a color varying from "avellaneous" to "wood brown" (Ridgway Color Standards and Nomenclature). Another variant at the same stage of growth has a color corresponding to "Saccardo's umber." A third is "mummy brown." In the case of these three variants no attempt will be made to describe in detail the gradual change in color from white through

various shades of pink to the final brown. The differences also become negligible when the culture begins to dry with age, when they all look practically alike. The distinct colors reappear when

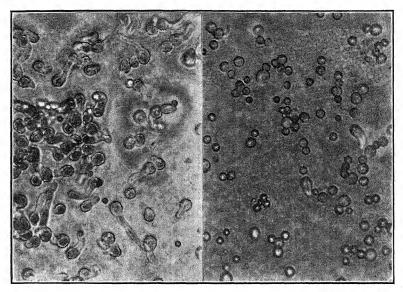


Fig. 2.

a new culture is grown to maturity. The fourth variant, which has occurred only twice, is much more striking than any of the others. Early in its development the mycelium of this form shows a brilliant "citron yellow" color. As the culture matures, its older portions become "pyrite yellow" in color. The mature spores are brownish in color and much darker than the mycelium. last variant to be mentioned is much larger than any of the others from the earliest stages of its growth. It grows much faster than either the parent Aspergillus or any other variant and forms a much more luxuriant mycelium than the others. Spore formation, however, occurs later here and the sporangiophores are not as numerous. The spores of this "giant" variant have the same black color as those of the type of the species and in size are larger, having an average diameter of  $4\mu$ , in contrast to the  $3.5\mu$  of the species and all the other variants. This "giant" form has a much coarser appearance than the others (FIG. 3, central figure of the lower row).

Two other variants, mentioned earlier in this paper, may well be considered at this point. One of these was characterized by the pale grayish appearance it presented when mature. Microscopic examination of the first transfer showed its spores all more or less shriveled and abortive. Furthermore, the number of chains of spores growing on each vesicle was much less than the normal for the species. This variant did not long survive. The second variant was characterized by a complete absence of spores. Subcultures were repeatedly made from the mycelium and were grown under a variety of conditions, but none led to spore formation. Finally this form was discarded.

It will be noticed that, except in the "giant" and the sterile forms, the only character which distinguishes these variants from each other and the species is that of color. Measurement of spores shows no appreciable differences; to attempt comparative measurements of other parts seemed irrelevant in view of their variability. It is to be regretted that in the present study no measurements of such properties as respiration could be made; other interesting and significant effects might have been found.

As the work proceeded it seemed desirable to give some attention to the cytology of the various forms obtained. Very little work has been done here. Indeed, Wakayama (10) seems to be the only one who has made any extensive studies of the cytology of Aspergillus. He found that two chromosomes were present and described briefly the process of division of the nucleus in the sterigmata. The results of the present study are substantially in agreement with those of Wakayama.

To obtain material suitable for cytological study, spores were planted on agar and the cultures allowed to grow until mature spores began to show at their centers. Each culture was then cut into several sectors; and these were lifted from the agar and dropped into the fixing fluid. Several different fluids were used, including chromic acid-acetic acid mixtures, Bouin's fluid, absolute alcohol-acetic acid, and others. If the sector of mycelium did not sink immediately into the fixing fluid it was first put into warm water and pumped, until sufficient gas had been removed to cause sinking. It was then transferred to the fixing fluid. After fixing, the sectors were washed and embedded in paraffin. The

thickness of most of the sections was  $5\,\mu$ ; of a few,  $7\,\mu$ . The principal stain used was Heidenhain's iron-alum-haematoxylin, without counterstain. Other stains were used, but they showed nothing more than did the haematoxylin. The principal results

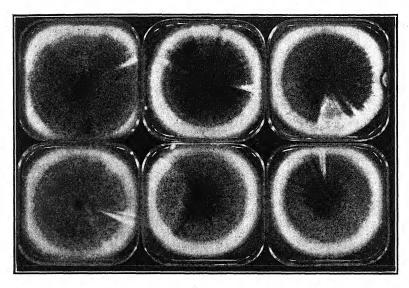


Fig. 3.

found in this cytological study are shown in figure 4, all the parts of which are drawn to the same scale.

Examination was confined mainly to the development of the spore-bearing parts, or sterigmata. When first formed these are minute spherical bodies thickly studding the entire surface of the vesicle. Each of these receives a single nucleus and elongates rapidly. There then occurs a nuclear division, various stages of which are shown in figure 4a and in the two right-hand parts of 4b. No significance is to be attached to the distinctly different sizes of the primary sterigmata at the time of nuclear division, nor does there seem to be any definite position for the nucleus. The two resulting nuclei always appear approximately at opposite ends of the sterigmata. The outer part of the primary sterigma is cut off to form the secondary sterigma, a condition which was frequently observed in its early stages. (The three left-hand parts

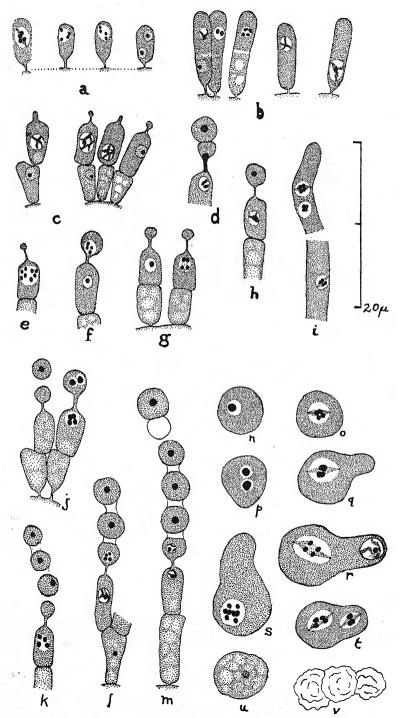


Fig. 4.

of Fig. 4b.) The nucleus in the secondary sterigma divides at once, often starting to divide before the division of the sterigma itself is complete. Figure 4c further shows stages in the division of the nucleus and also the initial stages of spore formation. At the left is illustrated what is probably the initial stage in the development of the second of the two secondary sterigmata commonly present on the primary sterigma of this species of Asperaillus. Figure 4d shows the apical portion of a secondary sterigma, from which one spore is already cut off, and another is forming and receiving a nucleus from the sterigma, while the remaining nucleus in the sterigma is already well advanced in another division. Very few cases were found in which a sterigma of the "giant" form had the chromosomes sufficiently separated to be distinguished. Examination of these indicates that in this form the number is twice that found in the species and in all the other variants (FIG. 4e). Nearly all the sterigmata of the "giant" form examined had the minute chromosomes so compactly massed that it was impossible to determine the number. Quite often the nucleus divides (FIG. 4f, l, m) after it has passed into the immature spore and an immature spore is binucleate (Fig. 4i). Since all the mature spores of this species seem to be uninucleate it may with reason be asked whether such a binucleate immature spore divides or whether the second nucleus has some other fate. The present study unfortunately yielded no information on this point. Figures 4q, h, k, l and m show additional stages of spore formation and nuclear division.

Divisions of the nuclei in the tips of the hyphae were frequently observed. In all these, two chromosomes were found (FIG. 4i). Except when these chromosomes were separating in anaphase, they were so close together that it was impossible to make out any details clearly. In no case was it possible to determine the number of chromosomes present in nuclei dividing in the tips of the mycelium of the "giant" form.

Because of the irregular ratio of development of the spores which were irradiated at 12 kv., it seemed desirable to attempt to examine them cytologically. To do this they were allowed to grow seven hours. Then, by pressing a fine needle gently against the surface of the agar, a few of the spores were pushed down into

the agar slightly. Small blocks of the agar into which spores had thus been pressed were cut out and treated in the same way as the material described above. Hundreds of spores were thus embedded, sectioned and studied. Some of these are shown in figures 4n to v.

At the time of fixation many of the spores had swollen considerably but still contained only one nucleus which showed no sign of dividing (Fig. 4n); other spores swollen about as much contained a dividing nucleus, with two chromosomes present (Fig. 40). Such swollen spores soon became binucleate and at the same time showed the first indication of germ tube development as a small bulge from the surface of the spore (FIG. 4p). Frequently the development of the germ tube was well advanced before nuclear division in the spore was completed (FIG. 4q). As germination of the spores proceeded and the germ-tube elongated, divisions of the nuclei followed one another in rapid succession (FIG. 4r, t), each nucleus showing quite distinctly its two chromosomes, especially when the latter separated in pairs during anaphase. Of all the spores examined, only two were found to differ; in these the number of chromosomes present in the dividing nucleus was found to be twice the normal (FIG. 4s).

It is possible that these two spores showed the condition which led to the formation of the "giant" variant. In what way the doubling may have taken place is not apparent. Normally the growing spores had a uniformly dense homogeneous cytoplasm. In contrast to the normal spores, there were many in which the cytoplasm was extremely vacuolate (FIG. 4u). A few of these spores still contained a nucleus, which stained very faintly, but most of them showed no sign of any such body. Eventually these spores lost all their cytoplasmic content while at the same time the wall became very much wrinkled and the entire spore shriveled up (FIG. 4v). These spores apparently had gone through the preliminary stages of growth, swelling considerably, but never developed further.

The stages shown in figure 4 represent the principal phases in the development of the spores and the history of the division of the nuclei. Many additional stages were observed in all the vari-

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ants described above, as well as in the species, but little else of significance was seen.

#### SUMMARY

Irradiation of spores of Aspergillus niger has produced several variant strains of this fungus. These strains differed markedly from the parent, most commonly in the color of the fruiting mycelium. One showed an evident increase in size. They have been continued through several asexual generations without showing any appreciable change. Calculations indicate that at the voltage used (ca. 12 electron kilovolts) the electrons penetrate the spores far enough to release most of their energy in the zone in which the nucleus is located. This suggests that the observed effects are a result of changes in the nucleus and that they may therefore be considered mutations. A cytological examination of the different variants showed only one evident nuclear change; in the large variant the number of chromosomes was twice that of the normal form. Otherwise the cytology of all the variants and of the species was alike. Several repetitions of the work gave comparable results, producing variant forms of apparently identical nature.

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#### EXPLANATION OF FIGURES

- Fig. 1. Spores in the region of the edge of the radiation band, those above the line which indicates this edge were rayed, those below unrayed. The dosage in this case was heavy, the voltage fairly low.
- Fig. 2. Radiation effect on spores receiving of electrons of 11.52 ekv. energy, showing great irregularity of germination at the right, compared with control spores at the left.
- Fig. 3. Mature cultures from groups of ten spores or less, showing variant sectors. The sector (center of the lower row) shows the large form. The other sectors are conspicuous because of their light colors, contrasting sharply with the normal black *Aspergillus*.
- Fig. 4. a, stages in division of nucleus in primary sterigmata; b, stages in division of nucleus in primary sterigmata (2 right hand); stages in division of secondary sterigmata (3 left hand); c, nuclear divisions and early stages of spore formation; d, apex of sterigma and spores, nucleus migrating and nucleus dividing; e, nucleus in sterigma of "giant strain"; f, division of nucleus in immature spore; g, anaphase condition of nuclear division in secondary sterigma; h, prophase condition of nuclear division in secondary sterigma; i, hyphal tips with dividing nuclei; j, immature spores, one of which contains two nuclei; k, chain of uninucleate spores attached to secondary sterigma in which the nucleus shows distinctly the two pairs of

chromosomes; l, m, chains of spores, in the youngest of which a nuclear division is taking place while the nucleus remaining in the secondary sterigma is also dividing; n, much swollen spore containing a single nucleus; o, much swollen spore with nucleus dividing, and showing two chromosomes; p, binucleate swollen spore with germ tube just starting; q, germinating spore containing a single dividing nucleus; r, t, germinating spores each with two dividing nuclei; s, germinating spores in which there is twice the usual number of chromosomes present; u, spores containing vacuolate cytoplasm and a faintly staining nucleus; v, spores with much wrinkled walls and containing no cytoplasm.

# HETEROTHALLISM IN CERATOSTOMELLA MULTIANNULATA

Ross W. Davidson

A number of workers have reported a variety of reactions in attempts to determine sexual processes in species of *Ceratostomella* as was pointed out by Leach <sup>1</sup> in 1934. At the suggestion of Andrus, a similar study was made to determine whether *C. multi-annulata* Hedge. and Davidson was heterothallic. This study was referred to by Andrus in 1936 <sup>2</sup> but was never published in detail. The results which were from single-ascospore and single-conidium cultures may be of interest to other workers and are recorded here.

Nine single-conidium cultures of C. multiannulata were secured from a perithecium-producing colony. None of these cultures produced fertile perithecia, but upon making all possible crosses with them, one of them formed perithecia when crossed with each of the other eight. Eight single-ascospore cultures were then obtained, none of which formed fertile perithecia. Four of these formed fertile perithecia when crossed with any one of the other four. The results of all possible crosses of these single-ascospore and single-conidium cultures are shown in Table 1. These results show that C. multiannulata is heterothallic with two sex groups represented, one comprising isolates No. 9 from a conidium and Nos. 10, 11, 12 and 13 from ascospores, and the other group the rest of the single-spore isolates. All intra-group crosses produced no perithecia and all inter-group crosses produced perithecia in abundance along the line where the mycelium of + and strains grew together.

A few abnormally long-beaked perithecia developed in some of these single-spore cultures, but none was found to contain ascospores. The beaks of these sterile perithecia ended in tufts of

<sup>&</sup>lt;sup>1</sup> Leach, J. G. The production of perithecia in *Ceratostomella ips* Rumb. Phytopath. 24: 1037-1040. 1934.

<sup>&</sup>lt;sup>2</sup> Andrus, C. F. Cell relations in the perithecium of *Ceratostomella multi*annulata. Mycologia 28: 133-153, 1936.

## TABLE 1

ALL POSSIBLE PAIRINGS OF 9 SINGLE-CONIDIUM CULTURES AND 8 SINGLE-ASCOSPORE CULTURES OF Ceratostomella multiannulata HEDGCOCK AND DAVIDSON

+	indicates	fertile	perithecial	production;	-, 1	no	fertile	perithecia.
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	Single-conidium cultures									Single-ascospore cultures								
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
	1	_	_	_	-	-	-	-	-	+	+	+	+	+	-	_	-	_
ures	2	_	-	-	_	-	-	-	-	+	+	+	+	+	_	_	-	_
cult	3	_	-	-	-	-	-	_		+	+	+	+	+	_	-	_	
ium	4		_	-	_	-	-	_	_	+	+	+	+	+	_	-	_	
Single-conidium cultures	5	_	_	_	-	_	_	_	_	+	+	+	+	+	_	_	_	_
gle-c	6			_	_		_	_		+	+	+	+	+	_	_	_	_
Sing	7		_	=	_	_	_	_		+	+	+	+	+	_	_	_	_
	8	_	_	_	_		_	_	_	+	+	+	+	+	_	_	_	
	9	+	+	+	+	+	+	+	+	_	_	_		_	+	+	+	+
	10	+	+	+	+	+	+	+	+	_	=	_	_	_	+	+	+	+
ro	11	+	+	+	+	+	+	+	+	_	_	_	_	_	+	+	+	+
ture	12	+	+	+	+	+	+	+	+	_	_	_	_	_	+	+	+	+
cul	13	+	+	+	+	+	+	+	+	_	_	_	_	_	+	+	+	+
spore	14	=	_	_	_	_	_	_	_	+	+	+	+	+	_	_	_	_
Single-ascospore cultures	15	7		_	_	_	_		_	+	+	+		+	_	_	-	_
ıgle-a	16	_	_	_	_	_	_	_	_	+	+	+		+	_	_	_	_
Sin	17	_	_	_		_	_	_	_	+	+		-	+	-	-	_	-

brown hyphae instead of the short hyaline bristles found on normal ones.

The fact that this species develops an abundance of perithecia in a few days makes it easy to demonstrate this heterothallic condition. However, it is possible that single-spore cultures from other mass isolates would not always react in the same way.

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# WHITE PERITHECIA AND THE TAXON-OMY OF HYPOMYCES IPOMOEAE

## WILLIAM C. SNYDER

In the course of studying a Fusarium root and fruit rot of cucurbits (4), a number of isolates of the causal fungus, which agrees morphologically with the species F. javanicum Koord., were collected from infected plants (Cucurbita maxima Duchesne and C. Pepo L.), grown in various parts of California. Single spore cultures of each collection were tested for pathogenicity, and all were found highly pathogenic. It was observed that perithecial fundaments (primordia) appeared in most of these cultures after a period of about a month or more, and that in some cultures they were red and in others white. In no case, however, did any of these primordia develop into perithecia.

Following the lead of Zycha (6) and Dimock (1) who demonstrated heterothallism in *Hypomyces*, conidial suspensions were prepared from cultures bearing white primordia, and applied to those bearing red primordia, and vice versa. In less than a week the fundaments in the fertilized cultures were developing into perithecia. Of special interest, however, was the fact that the cultures bearing red primordia developed only red perithecia while those bearing white primordia developed only white perithecia. These results indicated first, that the fungus under consideration is heterothallic, and second, that perithecial color may be either red or white. In view of the emphasis given to the color of perithecia in taxonomic treatments of the Hypocreales, the latter point seemed sufficiently significant to merit further study.

Upon maturation of the red and white perithecia obtained by means of cross fertilization, the morphology of the two types was compared. Both were found to fall within the limits of Hypomyces Ipomoeae (Hals.) Wr. (5), one differing however in whiteness of perithecia and both in pathogenicity.

Single ascospore cultures were prepared from the red and from

the white perithecia, respectively. These developed into Fusarium colonies representative of the original isolates, and in inoculation tests were found to be pathogenic on cucurbits. Thus their identity with the original isolates was confirmed.

In the isolations from nature, the cultures with red primordia proved to have a sex-reaction opposite to those with white primordia. Therefore reciprocal crosses of these types gave fertile perithecia, the color of which was dependent upon the direction of the cross. Approximately half of the single ascospore cultures from such a cross, whether taken from red or from white perithecia, developed red fundaments and the remainder developed white fundaments. The sex-reaction, however, was inherited independently of primordial color, so that it was possible to obtain fertile matings between types having only red fundaments, and also with those having only white fundaments. Reciprocal crosses involving only the one type of primordium as to color yielded only one kind of perithecial color independently of the direction of the cross.

These results showed definitely that not only are the red and white perithecial types interfertile, but that the stable color of the primordium (and therefore of the perithecium) is inherited. No intermediate types of perithecial color have resulted in any of the crosses, nor has more than one type of primordium appeared in any one single spore culture. The additional facts that the progeny from both red and white perithecia are all highly pathogenic on squash, and that all have the same morphology demonstrate beyond question that only one fungus is involved. Single ascospore cultures of this fungus then belong to two sex-reaction groups and may be described as being self-sterile, inter-group fertile, intragroup sterile, and hermaphroditic.

Although it is known that changes in perithecial color take place on aging, such as the change from red to brown or white to honey color, here the two types have remained distinct throughout their development. It has not been possible to change the one type into the other by means of aging, nor by the application of acid or alkali to them.

The occurrence of both red and white perithecia in the perfect stage of one and the same fungus, is particularly significant in respect to taxonomy. Color as a taxonomic character has been used extensively in the past. More recently the trend has been to discount the value of color as a taxonomic criterion and to emphasize morphology especially in the imperfect genus Fusarium (3). This trend, however, has not become so marked where perfect fungi are concerned. The finding reported here that in H. Ipomoeae perithecial color is inheritable and may be red or white (perhaps additional isolates of the fungus will reveal other types of perithecial color) emphasizes the hazard in using color as a taxonomic character, even in the fruiting structures of perfect fungi.

H. Ipomoeae is not uncommon in its occurrence on decaying plant tissues, especially in warm climates. Most frequently it is known only as a saprophyte. An account of the disease of cucurbits referred to here, caused by a form of the above fungus, will appear elsewhere.

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# A NEW POWDERY MILDEW

FRED J. SEAVER

(WITH 1 FIGURE)

During the autumn of 1939 the writer, while wandering through the conservatories of The New York Botanical Garden in search of material for class study on the fungi, observed a powdery mildew in full fruit on a rather unusual host.

The host proved to be *Jaborosa integrifolia* Lam., an Argentine plant. On checking up the material it was found that this host had been brought to The New York Botanical Garden by John K. Small and Edward J. Alexander from Louisiana in 1930, where the South American host had become established as a weed. It belongs to the family Solanaceae.

Whether the fungus came with the host plant from South America, or was acquired after the host had been brought up here is impossible to know. Or, again, whether the fungus was acquired in the greenhouse, or came with the host from Louisiana is uncertain.

The fungus belongs to the genus *Uncinula*. No powdery mildew has ever been reported on this plant, and the fungus appears to be different from any that the writer has seen described. It is characterized by its exceedingly long appendages, four or five times as long as the diameter of the perithecium. Since the fungus appears to have been unrecorded heretofore, the writer ventures to offer it as a new species.

# Uncinula Jaborosae sp. nov.

Myclium occurring on both sides of the leaf but more copious on the upper side forming more or less confluent patches; perithecia abundant usually thickly gregarious near the center of the mycelial patches, reaching a diameter of  $120 \,\mu$ ; appendages usually not exceeding 25, reaching a length of 4–5 times the diameter of the perithecium, subhyaline or very faintly colored, with a definite

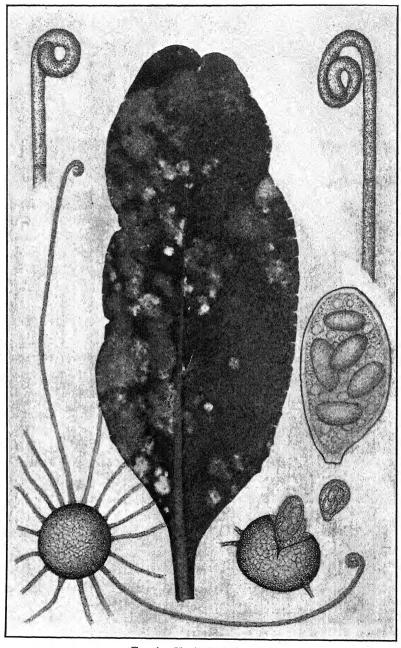


Fig. 1. Uncinula Jaborosae.

coil at the tip; asci several to each perithecium ellipsoid 46–50  $\times$  65–70  $\mu$ ; spores about 5 to each ascus, ellipsoid 10  $\times$  20  $\mu$ .

On leaves of *Jaborosa integrifolia* Lam. in the greenhouse of The New York Botanical Garden, Dec. 15, 1939.

Amphigena; peritheciis sparsis vel gregariis, minutis,  $120 \,\mu$  diam.; appendicibus copiosis (15-25), longioribus (480-600  $\mu$ ) subhyalinis; ascis 46-50  $\times$  65-70  $\mu$ ; sporis 5, ellipsoideis,  $10 \times 20 \,\mu$ .

THE NEW YORK BOTANICAL GARDEN

# MORENOELLA QUERCINA, CAUSE OF LEAF SPOT OF OAKS

E. S. LUTTRELL 1

(WITH 13 FIGURES)

#### INTRODUCTION

A leaf spot disease caused by Morenoella quercina (Ellis & Martin) Theissen occurs on oaks within the Duke Forest. Although this disease is very common here, it has not previously been made the subject of special study. Furthermore, the developmental history of the pathogene is unknown and from a survey of mycological literature it is apparent that there is a scarcity of information regarding other related Microthyriaceae. These considerations led to a study of this disease and of the life history of its causal fungus, the results of which are presented in the following account.

#### SUSCEPTS AND RANGE OF THE DISEASE

Northern red oak, Quercus borealis Michx. var. maxima (Marsh) Ashe and black oak, Q. velutina Lam. are the principal suspects although the disease is frequently found on blackjack oak, Q. marilandica Muench., scarlet oak, Q. coccinea Muench., southern red oak, Q. rubra L., and willow oak, Q. phellos L. The comon white oaks, Q. alba L. and Q. stellata Wangenheim appear to be immune. Collections of Morenoella quercina in the Mycological Herbarium of the U. S. Department of Agriculture

<sup>1</sup>I wish by this means to thank Dr. Frederick A Wolf, Botany Department, Duke University, for suggesting the problem and for his advice and criticism during the course of the study and in the preparation of the manuscript.

I am also indebted to Dr. David H. Linder, Harvard University, and to Dr. William W. Diehl, U. S. Department of Agriculture, for information concerning collections of *Morenoella quercina* in the Farlow Herbarium and in the Mycological Herbarium of the U. S. Department of Agriculture, respectively.

and the Farlow Herbarium show that the fungus has been found elsewhere on the red oaks, Q. rubra L., Q. pumila Walter, and Q. myrtifolia Willdenow, and on the white oaks, Q. geminata Small, Q. virginiana Miller, Q. virens Aiton, Q. minima Small, Q. Chapmani Sargent, and Q. stellata Wangenheim. The fact that here M. quercina is restricted to red oaks while in other regions it has been found on white oaks as well, suggests the existence of different strains of the fungus capable of attacking the various species of oaks. The geographical range of M. quercina as shown by the above collections, is the southeastern United States for it has been collected in the District of Columbia, Virginia, North Carolina, South Carolina, Florida, Louisiana, Mississippi, and Texas.

## APPEARANCE OF THE DISEASE

The disease is most conspicuous on seedlings and small trees, frequently involving a considerable percentage of their total leaf The first symptoms may be found in early summer when small blackened areas appear on the leaves. At this stage, unless examined microscopically, the lesions may be confused with injury produced by sucking insects. This leaf spot may be readily identified in any stage of its development, however, by the characteristic mycelium of Morenoella quercina on the upper leaf surface. Freehand sections cut parallel to the surface and examined under the microscope are the best means of determining this feature. The disease progresses slowly throughout the summer, but during September the spots rapidly increase in size until they reach diameters of a centimeter or more. On the upper surface they are roughly circular and are purplish black in color, while on the lower surface they appear as irregular, brownish discolored areas (FIG. 1). On severely infected leaves the spots become confluent and often cover almost the entire leaf. There is no premature defoliation. Nevertheless, the photosynthetic activity of the leaves is seriously impaired during a period in which normally food reserves are being accumulated in the stems and roots. A lowering of the vitality of seedlings as a result of severe infection for several successive seasons is the most serious consequence of the disease that could be expected. It is of no appreciable importance on older trees.

## TAXONOMY OF THE PATHOGENE

The causal fungus is identical with Aulographum quercinum (also spelled Aylographum or Ailographum) which Ellis and Martin (2) described in 1883 on the leaves of Quercus virens. Tracy and Earle (17) transferred this species to the genus Lembosia in 1895 because the ascospores become dark brown at maturity. Both Aulographum and Lembosia were included in the

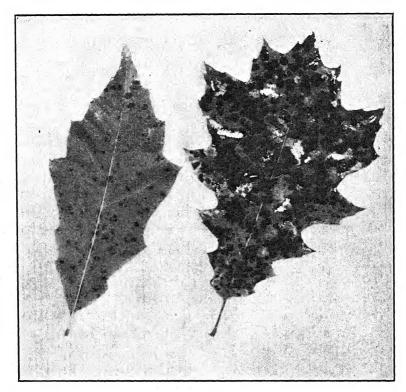


Fig. 1.

family Hysteriaceae, order Hysteriales. In 1883 Speggazini (13) created a new genus, *Morenoella*, and placed it in a new family which he called Hemihysteriaceae. Theissen (14) was able to find little difference between the genera *Morenoella* and *Lembosia* although they had been assigned to different families. He regarded both genera as having closest affinities with the Micro-

thyriaceae and, accordingly, in 1913 placed them in that family, maintaining them as separate genera, however, on the basis of the presence or absence of paraphyses. He emended the description of Lembosia to include only paraphysate forms, the forms lacking paraphyses being united under Morenoella. On this basis of separation Lembosia quercina (Ellis & Martin) Tracy & Earle became Morenoella quercina (Ellis & Martin) Theissen. In the same year Theissen (15) created the new family, Hemisphaeriaceae, which he united with the Microthyriaceae in a new order, the Hemisphaeriales. In 1917 (16) in a more extended treatment of the Hemisphaeriales, he expanded the order to include the Stigmateaceae, Polystomellaceae and Trichopeltaceae in addition to the two above-mentioned families. Members of Theissen's Polystomellaceae are included in the Microthyriaceae by Arnaud (1) who removed this family to a separate order, the Microthyriales coordinate with the Hemisphaeriales.

## STRUCTURE AND DEVELOPMENT OF THE PATHOGENE

In studying the development of the fungus only material from the leaves of *Quercus borealis maxima* was used. This was done to obviate confusion that might arise if different strains of the pathogene occur on different host species. Freehand cross sections and sections cut parallel to the surface were mounted in lactophenol in which 0.5 per cent cotton blue had been dissolved. By this means observations of the progressive development of the pathogene could be made frequently. To supplement these observations bits of infected leaf were fixed in acetic-alcohol solution at appropriate intervals, embedded in paraffin and sectioned at a thickness of  $5 \mu$ . The sections were stained with Haidenhain's iron alum haematoxylin and counterstained with Orange G in clove oil.

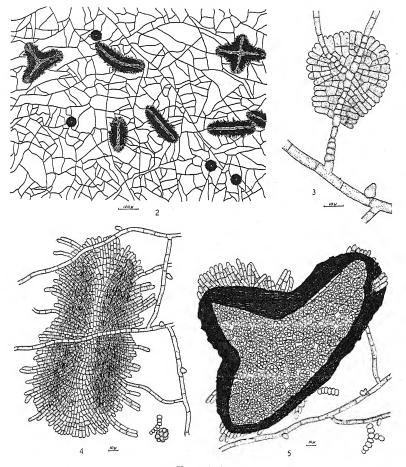
The Mycelium. The mycelium is restricted to the upper surface of the leaf and is entirely superficial, at least during the major portion of the summer. In cross sections of the infected leaf the hyphae are seen resting on the surface of the cuticle which appears to be intact and unaffected by the activity of the fungus. Nevertheless, the epidermal and mesophyll cells immediately beneath the hyphae are brown and disorganized. Ultimately the tissues ex-

tending from the upper to the lower leaf surface become necrotic. At this stage sections cut parallel to the surface show the mycelium radiating over the cuticle in all directions from the locus of infection. It is composed of dark brown thick-walled hyphae about  $4.5 \mu$  in diameter. Transverse septations divide the hyphae into cells 9-16  $\mu$  long. The hyphae branch and anastomose freely to form an open reticulum (FIG. 2). At intervals variously shaped ovoid to elliptical protuberances 6-9 µ long appear along the sides of the hyphae (Figs. 3-5). These protuberances are the hyphopodia. Their presence together with the anastomosing habit of the brown hyphae gives a distinctive appearance to the mycelium. Frequently hyphal branches break up into short chains of large rounded cells or toruloid hyphal fragments. These become scattered over the leaf surface and may function as conidia. rounded cells sometimes divide in several planes to form moruloid clusters (FIG. 4, 5).

In September hyaline hyphae appear beneath the cuticle. They are composed of large, irregular cells  $3{\text -}10\,\mu$  in diameter. Each contains a peripherally disposed network of chromatic material (Fig. 9). In cross sections these cells appear as groups of large, spherical vesicles lying between the cuticle and the outer epidermal walls (Figs. 6–8). They rapidly increase in number throughout the fall. In all sections examined, no morphologic connections between the external and the internal mycelium could be demonstrated. Nevertheless, the subcuticular mycelium is thought to be produced from the superficial mycelium because it develops only immediately beneath the latter.

The spermogonium. Spermogonia appear during August and are mature by the middle of September (FIG. 2). The mature spermogonium is hemispherical in shape with the flattened side appressed to the leaf surface. The wall is halved, consisting of a dome-like structure seated upon the leaf. A wall is lacking across the base of the spermogonium (FIG. 12). When observed in surface view the spermogonium appears to be made up of radiating hyphae although at maturity this feature is discernible with difficulty, except at the margins, because the wall becomes carbonaceous and opaque. At the center a pore or ostiole is formed by the separation of cells. In cross sections the upper wall

is seen to be composed of a single layer of darkened, thick-walled cells. This wall arches over a cavity whose floor is made up of a layer of large hyaline cells (FIG. 12). These cells are spermatiophores. Each cell is ampulliform in shape, the tapering apex



Figs. 2-5.

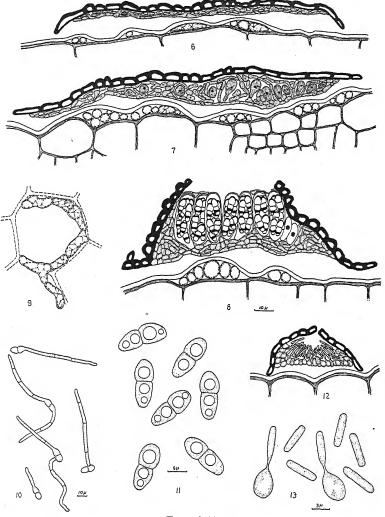
forming a sterigma, at the tip of which rod-shaped spermatia are abstricted singly (Fig. 13). Each spermatiophore probably produces several spermatia seriatim because the spermogonial cavity soon becomes filled with the bacilliform cells. The spermatia are hyaline and measure about  $6.4 \times 1.3 \,\mu$  (Fig. 13). They are

present from September throughout November being most abundant during October. After they are shed, the empty spermogonia remain in position until the leaves disintegrate.

The ascocarp. The formation of ascocarps is initiated while the leaves are still green and attached (FIG. 2). After abscission, an event which occurs about the end of November, the ascocarps continue development if the leaves fall in places which are not too dry. Early stages in ascocarp formation are found during September. Usually each ascocarp originates from a short segment of a single hypha. The segment becomes divided into a series of cells from the under side of which arises a group of hyphal branches that radiate in all directions over the surface of the leaf. They branch dichotomously and become fused laterally to form a flat, pseudoparenchymatous shield (FIG. 3). As a result of its origin from the under side of the hypha, this shield lies between the parent hypha and the leaf cuticle. The shield soon becomes black and carbonaceous so that its radiate structure can no longer be discerned except at the margins. Along its longitudinal axis a zone of lighter colored cells marks the line along which the shield is to split at maturity of the asci (FIG. 4). The shield varies in shape, being elliptical, Y-shaped, or in the form of a cross depending on whether the parent hypha was simple, branched, or crossed by another hypha at its point of origin (Fig. 2). During October hyaline branches originate beneath the shield and intertwine to form a compact plectenchymatous layer (FIG. 6). This layer extends beneath the entire shield but is only 2 to 3 cells in thickness.

Larger deeply staining hyphae, which are regarded as ascogenous hyphae, now appear within the plectenchymatous layer. It has been impossible to determine the origin of these hyphae. Terminal cells of branches of the ascogenous hyphae enlarge and become transformed directly into asci. The young asci are spherical and are scattered singly throughout the plectenchyma (FIG. 7). They are at first binucleate, but soon each contains only a single prominent fusion nucleus. Uninucleate asci may be found during January or sometimes as early as in December. The ascus elongates vertically and the fusion nucleus undergoes three successive divisions to form eight daughter nuclei. Around each of the daughter nuclei a membrane forms, delimiting the young asco-

spore. A large oil droplet forms in each end of the spore on either side of the nucleus. The nucleus divides and the resulting two nuclei move to opposite ends of the ascospore. A cross wall is



Figs. 6-13.

next laid down dividing the spore into two cells. The nuclei become indistinct, the chromatic material appearing as a peripheral band near each end of the spore. The ascospores continue to en-

large at the expense of the epiplasm until they reach at maturity a size of  $12\text{--}14 \times 5\text{--}6\,\mu$  (FIG. 11). They are now obovate in outline with the anterior cell somewhat larger in diameter and more rounded than the posterior one. Ultimately they become dark brown in color. The ascospores are clustered within the ascus which is short, cylindrical and broadly rounded at the apex, and is about  $27 \times 10\,\mu$  in size (FIG. 8). Most of the asci within an individual ascocarp mature at the same time. The asci are originally separated by strands of plectenchyma but as they enlarge this tissue is crushed and disintegrated so that the mature asci stand side by side on a basal plectenchymatous layer 2 to 3 cells in thickness (FIG. 8). As a result of increase in size of the asci the shield is raised and split along its longitudinal axis and the torn edges are pushed back exposing the layer of asci.

If leaves that have lain on the ground are collected in early March and placed in a moist chamber, ascospores may be matured within a week or two. If, however, the leaves remain out of doors, ascospore formation begins towards the end of March. Mature ascospores are present from April until June.

Germination of ascospores and growth in culture. Horne (7) reported that he was unable to obtain germination of ascospores in his attempts to culture Lembosia Rolfsii Horne, a fungus closely related to Morenoella quercina. According to Fisher (3) only a single species of the Microthyriaceae (she does not indicate its specific identity) has been successfully grown in culture. M. quercina, however, was easily induced to grow on artificial media. Ascospores were obtained by suspending portions of leaves bearing mature ascocarps from the cover of a Petri dish so that the spores were shed upon agar or upon a slide placed in the bottom of the dish. The ascospores germinated within 12 hours on agar or in drops of distilled water placed on a slide or on the surface of an oak leaf. Germ tubes are produced either terminally or laterally from one or both cells of the ascospore. The walls are at first hyaline, but they soon turn light brown. The hyphae formed in culture are lighter in color and more irregular, and the hyphopodia are elongated and more pointed than in nature.

The fungus was grown on malt agar, on agar containing a decoction of oak leaves, and on synthetic agar. Although growth

was not very abundant, malt agar proved to be the most satisfactory medium tried. On this medium the fungus forms black, hemispherical colonies about a centimeter in diameter. Neither more extensive vegetative growth nor the formation of reproductive structures has been obtained in culture.

## DISCUSSION

The superficial habit of *Morenoella quercina* immediately raises the problem of its nutritional relationships. During the summer the mycelium is restricted to the surface of the leaf and, as has been stated, there is no evidence of penetration of the cuticle. Nevertheless, it is evident that toxic substances are produced by the fungus and that they must diffuse through the cuticle into the leaf since the host tissue beneath the mycelium is killed. This being true, it is reasonable to assume that nutrients would likewise diffuse outward through the cuticle from the leaf cells to the mycelium. It is conceivable also that movement of food materials may be facilitated by alterations in the permeability of the cuticle which the fungus might produce without causing any apparent structural change.

Later in the season mycelium appears beneath the leaf cuticle. A parallel case is provided by the related Lembosia Rolfsii on vanilla in which Horne (7) found a subcuticular inveelium beneath the superficial mycelium. In both cases connections between the external and the internal mycelium have not been observed. the other hand Arnaud (1) noted the presence of internal mycelium in the case of several other species of Microthyriaceae and has been able to demonstrate organic connections with the external mycelium. Such connections might be overlooked even in the examination of a large number of sections. It is concluded, therefore, that in M. quercina the subcuticular mycelium probably arises from the external mycelium and is connected with it. Evidence in support of this conclusion is afforded by the observation that the size of the lesions on oak leaves increases greatly in early September at a time coincident with the development of the subcuticular mycelium.

Morenoella quercina is a type of parasite which in its early development depends upon nutrients absorbed through the host

cuticle, but which later penetrates the cuticle and comes into more intimate contact with the host cells. There is, however, no evidence of penetration of the host cells by M. quercina although Arnaud (1) described the formation of haustoria by both the internal and external mycelia of many of the Microthyriaceae which he investigated. Maire (9) and Ward (18) have also shown that the mycelia of species of Asterina which remain superficial produce haustoria similar in structure to those of the Erysiphaceae.

Morenoella quercina is the second member of the Microthyriaceae in which the production of spermatia has been reported. Ward (18) previously described their formation in Asterina spissa Sydow. According to him erect clusters of delicate hyphae are produced on the mycelium and on the young ascocarps. Spindle shaped spermatia are abstricted from the tips of the erect hyphae. He was, however, in doubt as to the nature of these structures because of difficulty in determining their exact relation to the mycelium. Consequently it remains uncertain whether they actually constitute a stage in the life cycle of the Asterina. Although he made no mention of spermogonia in his text, Arnaud (1) figured, in a habit sketch of Morenoella mollenideae Arnaud, structures very similar to the spermogonia described for M. quercina. seems highly probable that spermogonial stages will be found in the life cycles of other members of the Microthyriaceae when collections are made at the proper season. The question of their function in this group of fungi must, however, be left unanswered for the present. In view of the common occurrence of functional spermatia in other groups of Ascomycetes it seems likely that they are functional also in the Microthyriaceae but this assumption remains to be demonstrated.

The structure of the ascocarp of *Morenoella quercina* shows that it can be regarded neither as a perithecium nor as an apothecium. It is purely vegetative in origin; consequently it may be considered a stroma differentiated into a covering pseudoparenchymatous layer and an inner plectenchymatous portion within which the asci develop. Each ascus originates individually and by its expansion creates a locule within the stroma. The fungus tissue between the asci is ultimately crushed and absorbed by the developing asci so that they form a continuous layer within one common locule.

The ascocarp of the Microthyriaceae was formerly considered to be a halved perithecium. According to Gaillard (4) Raciborski (11), and von Höhnel (5) the shield is the lower half of the wall of an inverted perithecium, the morphological base being attached to the hypha above and the apical part having disappeared through reduction in response to the protection afforded by the host leaf. Consequently, the asci, which grow upward with respect to the surface of the leaf, were considered to be inverted with respect to the perithecium. The fruiting bodies of the Microthyriaceae have, therefore, been frequently referred to as inverted perithecia and for such structures the term thyriothecium has been applied. Von Höhnel (6) later came to the conclusion that this conception of their structure is false. He decided that the fruiting body was composed of two parts: (1) a sterile shield which developed from the lower side of the mycelium and (2) an erect perithecium which developed beneath the shield. The wall of the perithecium was greatly reduced as a result of the protection afforded by the shield. All of these investigators were concerned chiefly with the structure of the shield. Ryan (12) from the reports by Gaillard (4), Raciborski (11), and von Höhnel (5) on the Microthyriaceae and from her own observations on members of eleven genera of this family recognized the occurrence of four developmental types. According to her account the shield may originate either form: (1) any cell of the mycelium, (2) a large nodulose cell in the mycelium, (3) a short hyphal branch, or (4) a hyphopodium. Of these types the first is the most common and, as has been shown, is the one found in Morenoella quercina.

The most complete developmental study in the Microthyriaceae hitherto made is that of Ward (18) on Asterina spissa. Although it is difficult to make a comparison on the basis of Ward's description, the structural development in Asterina spissa seems to be similar to that in M. quercina.

Development in Stigmatea Robertiana, a member of the related family Stigmateaceae, is essentially the same as in M. quercina. According to Killian (8) its mycelium forms a continuous subculticular plectenchyma. Local thickenings in the plectenchyma, formed by the horizontal division of the cells, develop into stromata. Within the stroma the asci arise individually from the as-

cogenous hyphae. He was also able to determine that the ascogenous hyphae originate from an ascogonium after its fusion with an antheridium both of which organs are formed within the stroma.

Nannfeldt (10) has divided the Euascomycetes into three subdivisions based on the type of ascocarp; the Plectascales, the Ascohymeniales and the Ascoloculares. The Plectascales includes all Ascomycetes in which the reproductive organs are produced free on the mycelium and after fertilization become enveloped by a layer of hyphae to form a closed ascocarp. The ascocarp may or may not have a definite external wall and within it the asci are iregularly distributed. In the Ascohymeniales a hymenium composed of asci and true paraphyses is formed within ascocarps initiated as a result of a sexual stimulus. The ascocarps may be free or formed within a stroma and are either perithecia or apothecia. In the Ascoloculares, the reproductive organs are differentiated within a stroma which is vegetative in origin and the asci are formed individually in locules which they create by their growth within the stroma. Nannfeldt assigned the Hemisphaeriales to the Ascoloculares. The results of the present studies on Morenoella guercina and those of Killian on Stigmatea Robertiana constitute evidence that these fungi should be included in the Ascoloculares. Additional and more complete developmental studies of other species are necessary, however, before any generalizations should be made for the Hemisphaeriales as the order is now constituted.

#### SUMMARY

A leaf spot disease of oaks caused by Morenoella quercina (Ellis & Martin) Theissen, present on oaks in the Duke Forest apparently occurs widely throughout the southeastern United States. This leafspot is found on the red oaks Quercus borealis maxima, Q. velutina, Q. rubra, Q. coccinea, Q. marilandica, and Q. phellos within the Duke Forest but does not infect the white oaks Q. alba and Q. stellata. Elsewhere it has been found on other oaks, both white and red. The disease causes a decrease in the photosynthetic activity of seedlings and young trees, lowering their vitality, but is of no appreciable importance on older trees.

Morenoella quercina is a superficial parasite which in its early development depends on nutrients absorbed through the intact host

cuticle. Later the hyphae penetrate the cuticle and form a subcuticular mycelium. The external mycelium sometimes produces toruloid hyphal fragments which may function as conidia.

M. quercina has a spermogonial stage which hitherto has not been described. Spermogonia and ascocarp initials are produced concurrently on the same external mycelium before the leaves are shed. The ascocarps continue development on the fallen leaves and reach maturity in spring.

The ascocarp is a flat stroma consisting of two parts: a pseudo-parenchymatous, radiate shield which originates from a segment of a single hypha, and a plectenchymatous fertile layer which forms beneath the shield. The asci arise singly within the stroma. In their development the intervening sterile tissue is crushed and absorbed. The covering shield eventually becomes cleft to expose the mature asci.

Morenoella quercina belongs in the family Microthyriaceae, order Hemisphaeriales, and is included in the group Ascoloculares as delimited by Nannfeldt.

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#### EXPLANATION OF ILLUSTRATIONS

Fig. 1. Northern red oak leaves bearing lesions produced by Morenoella quercing. (The leaf on the left viewed from the lower surface, the one on the right from above.); 2. Mycelium of M. quercina on the upper surface of lesion on oak leaf showing spermogonia and young ascocarps; 3. Surface view of young ascocarp showing the origin of the shield from a hyphal segment; 4. An ascocarp in a later stage of development; 5. A mature ascocarp; the shield has been cleft exposing the layer of asci. (Note hyphopodia on the mycelium in Figs. 3-5 and toruloid hyphae in Figs. 4 and 5.); 6. Cross section of a young ascocarp in which a plectenchymatous layer is forming beneath the shield; 7. Cross section of an ascocarp showing the young asci developing individually within the plectenchymatous layer; 8. Cross section of a mature ascocarp of M. quercina. (Hyphae of the internal mycelium are apparent between the cuticle and outer epidermal walls of the host cells in Figs. 6-8.); 9. Surface view of subcuticular mycelium; 10. Germinating ascospores; 11. Mature ascospores; 12. Cross section of a mature spermogonium of M. quercina; 13. Spermatiohpores and spermatia. Figs. 6, 7, 8, 9, and 12 drawn to scale indicated in Fig. 8.

# A NEW SPECIES OF PISTILLARIA ON RICE STRAW

RUTH E. REMSBERG (WITH 1 FIGURE)

An interesting fungus was found fruiting on rice straw from Louisiana, September, 1937. The straw had been placed in a moist chamber at room temperature. Abundant fruit bodies were observed within a week (Fig. 1). An examination of this fungus showed clearly that it belongs in the Clavariaceae. However, a search through the mycological literature on this family reveals no description to which it appears to conform.

Suggestions have been received regarding its disposition in the taxonomy of the fungi. Dr. G. W. Martin, of the University of Iowa, suggests that it be placed in the genus *Ceratella*, while Dr. J. N. Couch, of the University of North Carolina, thinks that it might be included in *Typhula*. A resumé of the taxonomic position of these two genera follows.

Quélet first recognized Ceratella as a distinct group of fungi (6), and made it a subdivision under the genus Clavaria to include those forms which were minute, unbranched and of a woody texture. Patouillard (4) elevated Ceratella to generic rank, using the characters, a pointed sterile apex and minute size, to distinguish it from other genera of the Clavariaceae. Quélet (7) retained Ceratella as a subdivision under Pistillaria, using the characters, an elongate clavula with a sterile pointed apex, to separate these species from the others. Saccardo (9) followed Quélet's example in disposing of these fungi. Patouillard (5) again preferred the generic rank, and used the fact that the hymenium surrounds only the middle portion of these minute plants as a basis for separation from the other genera of the Clavariaceae. He also mentioned that cystidia are present in the hymenial layer of Ceratella.

<sup>&</sup>lt;sup>1</sup> Letter written March 20, 1938.

<sup>&</sup>lt;sup>2</sup> Letter written December 24, 1938.

In later works on the Clavariaceae, *Ceratella* has been disposed of in various ways. Coker (2) does not recognize it as a genus. Bourdot and Galzin (1) follow Patouillard's example in giving it generic rank, while Killerman in Engler and Prantl (3) uses it as a subdivision under *Pistillaria*.

Although the fungus at hand frequently has a sterile pointed apex with the hymenium limited only to the middle portion of the plant, it does not seem wise to place it into *Ceratella*. The most obvious reason for excluding it from this genus is its large size. In all descriptions of *Ceratella* the species are minute, in fact, only a few millimeters tall. In addition, no cystidia are present in the hymenium of this fungus, while they are present in *Ceratella* (5). Furthermore, the position of *Ceratella* in the taxonomy is insecure, being accepted by some mycologists and rejected by others.

In my studies on the genus Typhula (8) I have proposed that all species having delicate, cartilaginous, club-shaped sporophores be placed either in Typhula, when a sclerotium is demonstrated to be present in the life history, or in Pistillaria, when a sclerotium is always lacking. The presence or absence of a true sclerotium seems to be the most reliable point of distinction between these two genera. Then all fleshy and large forms will be placed in Clavaria. With these facts in mind, I have placed this fungus in the genus Pistillaria where it may be included under the subdivision by those who wish to maintain the separation of those species with sterile tips.

# Pistillaria Oryzae sp. nov.

Sclerotia absens. Sporophori orientes e mattis hypharum laxe implexarum, ramosarum, septatarum, multis confibulis praeditarum; filiformi, cylindrici, simplices v. ramosi, subulati, attenuati gradatim ab basi leviter crassa in acutissimum apicem, non diversi in distinctum stipitem et clavulam, leviter pubescentes ad basim; 25–80 mm. alti; toti albi, dein colorati (anglice ochraceous buff to pinkish cinnamon) ut senescunt aut arescunt; hymenium aut per totam superficiem sporophori praeterquam ultimum apicem extentum, aut tantum per mediam partem apice et basi sterilibus; compositi ex hyphis, densis parallelis, interdum cocleatim positis, subhymenio denso, centro composito ex hyphis laxe implexis, septatis, ramosis confibulatis, parvulis crystallis incrustatis. Basidia clavata, leviter attenuata ad apicem, quadrispora; 27.23–35.01 µ longa, 7.78–9.73 µ lata. Sterigmata recta v. leviter curva, attenuata in gracilissimum apicem; 3–4 µ longa, 1.5–3.0 µ lata ad basim. Basi-

diospori ovati v. fusiformi, cum manifesta guttula, hyalini, glabri, apiculo manifesto, truncato; 5.06-7.78 × 8.95-11.67 μ, modus 6.48 × 10.88 μ. Hab. In foliis mortuis Orysae sativae, saprophytica ut videtur.

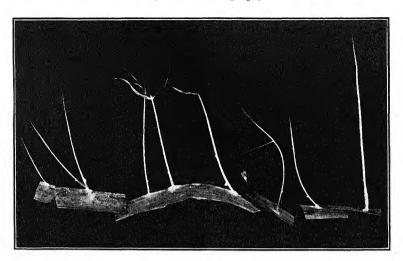


Fig. 1. Sporophores of Pistillaria Oryzae on dead leaves of Oryza sativa. ½ nat. size:11

Sclerotia absent. Sporophores arising from mats of loosely interwoven, branched, septate hyphae with numerous clamp connections; filiform, cylindrical, simple or branched, awl-shape, tapering gradually from a slightly broadened base into a very acute apex, not differentiated into a distinct stipe and clavula, somewhat pubescent toward the base; 25-80 mm. tall; entirely white, becoming light ochraceous buff to pinkish cinnamon with age or on drying; hymenium extending over either the entire surface of the sporophore except the extreme apex, or only over the middle portion the apex and base being sterile; composed of compact, parallel hyphae, sometimes spirally arranged, subhymenium compact, center composed of loosely interwoven, branched, septate hyphae with clamp connections, encrusted with small crystals. Basidia clavate, tapering slightly at the apex, 4-spored; 27.23-35.01 µ long, 7.78–9.73 µ broad. Sterigmata straight or slightly curved, tapering into a very delicate tip;  $3-4 \mu \log_{10} 1.5-3.0 \mu$  wide at the base. Basidiospores ovoid to fusiform, with a prominent guttula, hyaline, smooth, apiculus prominent, tuncate;  $5.06-7.78 \times 8.95-11.67 \mu$ , ave.  $6.48 \times 10.88 \,\mu$ .

<sup>&</sup>lt;sup>3</sup> Ridgway, Bobert. Color standards and color nomenclature. Washington, 1912.

HAB. On dead leaves of *Oryza sativa*, apparently saprophytic. Sporophores developed from leaves which had been placed in a moist chamber in the laboratory.

Type Material: 26861, on rice straw, Herbarium, Department of Plant Pathology, Cornell University.

Notes: The fungus was readily obtained in culture by fastening a sporophore in the lid of a petri dish and allowing the spores to be shot down onto agar in the bottom of the dish. The spores germinate within 24 hours, producing one or two germ tubes which rapidly elongate into septate, branched hyphae. The mycelial growth, which is very rapid in culture on potato dextrose agar and spreads in a characteristic fan-shape fashion, is abundant, white, aerial, and cottony. The fungus grows in culture from 6–33°C. or higher, with an optimum of 24–27° C. Fertile fruit bodies are produced abundantly in older cultures directly from the mycelium.

It was possible to obtain several crops of sporophores from the rice leaves in the moist chamber. After the first crop had matured, the leaves and chamber were placed in the refrigerator at 3° C. for 2–3 days and then removed to the laboratory. After 5–6 days new sporophores were produced. This was repeated five times, always obtaining 8–10 new sporophores.

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# STUDIES ON HISTOPLASMA CAPSULATUM AND SIMILAR FORM-SPECIES. II. EFFECT OF TEMPERATURE <sup>1</sup>

Arden Howell, Jr.<sup>2</sup> (with 8 figures)

In a preceding paper (3) the writer has shown that Histoplasma capsulatum Darling and Sepedonium chrysospermum (Bull.) Link resembled each other in their methods of spore formation and in the morphology of the aleuriospores, but that at the same time they differed in that Sepedonium chrysospermum produced phialospores, whereas Histoplasma capsulatum did not. Because of the fact that they seemed so strikingly alike on a morphological basis, and yet differed in the number of types of reproductive bodies formed, it became desirable to study the biology of these species. Histoplasma capsulatum Darling, which is parasitic on man, Sepedonium chrysospermum (Bull.) Link and Stephanoma tetracoccum van Zinderen-Bakker, which are parasitic on other fungi, and Sepedonium xylogenum Sacc., saprophytic on decayed wood were compared and differences in their responses to environment noted.

The first series of experiments is intended to determine the effect of temperature on the growth and sporulation of these fungi. In these experiments the fungi were grown on potato maltose agar made up according to the formula given in a previous paper (3). To insure uniformity of the medium, four liters of the potato decoction were made up at one time, and in order to obviate any

<sup>&</sup>lt;sup>1</sup> Contribution No. 184 from the Laboratories of Cryptogamic Botany and the Farlow Herbarium, Harvard University. The material presented here and in a previous paper (3) is a portion of a thesis submitted to the faculty of Harvard University, June 1939, in partial fulfillment of the requirements for the degree of Doctor of Philosophy in Biology.

<sup>&</sup>lt;sup>2</sup> The author is deeply indebted to Dr. David H. Linder, under whom these investigations were conducted, for his constant advice and encouragement, and for his assistance in the preparation of the manuscript. He also expresses his gratitude to Dr. William H. Weston, Jr., for his many helpful suggestions and criticisms.

carry-over effects of the inoculum, the fungi were grown on the stock experimental medium at room temperature. Uniform blocks of the medium, approximately two millimeters in diameter, taken from the advancing edge of the colony, were used as inoculum. Three such blocks were inverted on equidistant points on each Petri dish, and three similar plates were used for each species at each

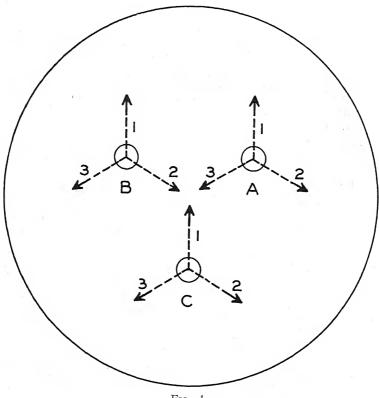


Fig. A.

temperature. The cultures were then placed at the various temperatures employed.

The diameters of the colonies were used as an indication of the amount of growth. These were measured in three directions on each colony and care was taken to measure the same diameters each time the measurements were made. This was accomplished by pasting small, circular pieces of paper, with arrows pointing in

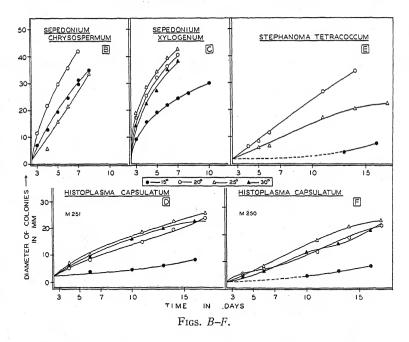
# HOWELL: HISTOPLASMA CAPSULATUM

TABLE I Effect of Temperature on Growth

	Temperature:										
Time in days	15°	c.	20	o ·	25	0 ,	30	37°			
3	A	В	A	В	A	В	A	В	A		
Sepedonium								,			
chrysospermum 3	7.06	0.93	11.81	1.35	0.00		0.00		0 0		
$\overset{\circ}{4}$	12.94	1.04	22.02	1.61	5.91	1.60	0.00		0.0		
5 6	19.44	1.17	29.70	1.55	16.02	3.45	0.00		0.0		
6 7	24.47	1.21	35.50	1.81	21.36	2.73	0.00		0.0		
8	31.13 35.16	1.36 1.95	42.06	3.64	29.98 33.90	3.51	0.00		0.0		
16	*	1.,,0	*		*	0.00	0.00		0.0		
Sepedonium xylogenum											
3 4	9.41	2.59	17.63 25.52	2.38	18.55 28.57	1.37	15.01 22.37	1.60 2.98	0.0		
5	19.24	2.03	32.08	1.72	34.12	1.84	27.22	3.04	0.0		
6	21.82	1.99	36.61	2.27	39.42	2.37	35.04	2.03	0.0		
7	24.57	1.76	40.46	3.79	42.55	3.14	38.39	2.60	0.0		
8 10	30.30	1.42 3.33	*		*		*		0.0		
16	*	3.33	*		*		*		0.0		
Stephanoma tetra-									0.0		
coccum	0.00		6.42	0.02	0.00		0.00		•		
4 5	0.00		6.43 8.35	0.93	0.00 6.05	0.80	0.00		0.0		
6	0.00		11.09	1.00	6.80	1.08			0.0		
11	0.00		26.25	2.30	16.98	2.27	0.00		0.0		
14	0.00		34.00	4.21	20.00	3.76	0.00		0.0		
16 17	7.64	1.11	*		22.35	3.53	0.00		0.0		
Histoplasma capsu-	*				22.33	3.33	0.00		0.0		
latum M 251											
3	0.00		0.00	0.45	4.13	1.14		004	0.0		
$\frac{4}{6}$	0.00		6.01 8.35	0.45	6.44 9.98	0.14 0.13		0.94 1.55	0.0		
10	4.97	0.64		0.02	9.90	0.13	15.59	1.41	0.0		
11			15.10	0.73	18.62	0.90			0.0		
13	6.62	0.52	10.50		20.40		20.06	1.38	0.0		
14 16	8.43	0.10	19.50	0.61	22.48	1.66	22.33	2.23	0.0		
17	0.43	0.10	24.00	0.69	25.11	1.65	22.33	2.23	0.0		
Histoplasma capsu-											
latum M 250	0.00		4.54	0.65	4.40	0.07	4.04	0.54			
$\frac{1}{6}$	0.00		4.54 6 70	0.65		0.87		0.56	0.0		
10	4.77	0.43	0.0	0.01	7.01	0.09	13.28	0.50	0.0		
11	-		14.00	0.81	17.90	0.78			0.0		
- 13	6.48	0.63	10.00	0.55	00.01	0.00	16.29	2.27	0.0		
14 16	8.22	0.67	19.02	0.55	22.91	0.99	21.75	1.72	0.0		
10 17	0.22	0.07	23.90	0.61	25.65	2.13		1.72	0.0		

three directions, on the under side of each Petri dish (FIG. A). Each colony was designated by a letter, and the diameters measured along lines 1, 2, and 3. This has the advantage of constant measurements, but in spite of this degree of standardization, as the colonies increase in size and approach each other or the edge of the Petri dishes, there is evidence of pronounced inhibition of growth which results in shortening the radii at various points on the periphery of the colonies, a fact which makes the standard deviations so high (Table I).

The results obtained are shown in part in Table I and Figures B-F. A study of these results shows that the optimum temperature, under the conditions of this experiment, for *Sepedonium* 



chrysospermum is 20° C.; that for Sepedonium xylogenum is 25° C.; that for Stephanoma tetracoccum is 20° C.; that for Histoplasma capsulatum is 25° C. whereas the maximum temperature at which growth occurs is between 25 and 30° C. for Sepedonium chrysospermum and Stephanoma tetracoccum, and lies between 30 and 37° C. for the remaining species. Although Sepedonium

xylogenum grew well at 30° C., its optimum was 25° C. Furthermore, it grew better at 20° than at 30° C. (FIG. C, H). On the other hand, Histoplasma capsulatum, for which the optimum temperature for growth was 25° C., grew almost as well at 30° and less rapidly at 20° C. It should be further pointed out that the growth curves of the two species of Sepedonium are somewhat similar (FIG. B, C) but in both cases are much greater than that of the two strains of Histoplasma capsulatum (FIG. D, F). Stephanoma tetracoccum takes a more or less intermediate position as regards rate of growth and shows more pronounced effects of temperature as may be determined from the fact that the growth curves are more distantly separated than in the other species (FIG. E). The two strains of Histoplasma are essentially identical in their rates of growth, both being extremely slow. It is also interesting to note that the rates of growth of Histoplasma capsulatum in this experiment are essentially similar to those reported by Moore (4) for another parasitic fungus in its saprophytic phase, Endomyces capsulatus Rewbridge, Dodge & Avers (Blastomyces dermatitidis Gilchrist & Stokes, 1898<sup>3</sup>).

It should be emphasized, however, that the diameters of the colonies do not always indicate accurately the amount of growth of the fungi. This is very evident in Sepedonium chrysospermum (FIG. B, G) in which form the greatest radial growth at any time during the course of the experiment occurred at 20° C., the next greatest at 15° C., and the least at 25° C. However, the colonies at 15° C. were characterized by scanty aerial mycelium whereas at 25° there was produced a very dense, cottony, aerial growth, which more than compensated for the smaller radial spread (FIG. G). Were it not for the fact that at 20° C. the radial growth was greatest and sporulation earliest, the density of the mycelium of the colonies at 25° would lead one to suspect that 25° were the optimum, but in determining the optimum conditions for growth it seems to the writer that time of sporulation is an equally important factor, at least as regards the perpetuation of the species in nature. For example, at the end of eight days' growth, cultures of this species at 15° showed only a few phialophores, simple or with

<sup>&</sup>lt;sup>3</sup> Benham, R. W.: The Fungi of Blastomycosis and Coccidioidal Granuloma. Arch. Derm. & Syph. 30: 385-400. Sept. 1934.

but few branches, in a colony. After the same length of time, cultures maintained at 25° showed dense masses of well-developed phialophores. Likewise, cultures of this fungus maintained at 20°

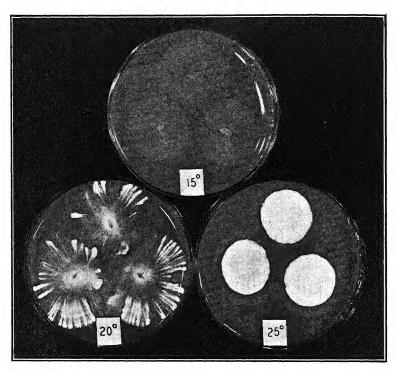


Fig. G. Sepedonium chrysospermum (Bull.) Link.

showed abundant phialophores and phialospores, but these were produced only on the radiate, aerial portions of the colonies (FIG. G).

Similarly, the aleuriospores, in cultures of Sepedonium chrysospermum, made their appearance first in those cultures grown at 20° C., and finally in those grown at 25°. Eventually, and only after a considerably longer period of growth, the greatest abundance of these spores was found in the cultures maintained at 25° and the least quantity in those at 15°. In contrast with this, aleuriospore production in Sepedonium xylogenum, Stephanoma tetracoccum, and Histoplasma capsulatum was correlated from the first with the abundance of the mycelium. This condition is

similar to that reported by Brown (1) for species of Alternaria, Botrytis, Fusarium, and other general in which he found that "with any particular medium the type of growth produced by the same fungus is very similar under the different conditions of the experiment, whether in air or in different concentrations of carbon dioxide, or whether at laboratory temperature or in cold store." In such cases measurements of the diameters of the colonies were good indications of the total amount of growth.

Because of the fact that in its parasitic phase Histoplasma capsulatum grows at body temperature or 37.5° C., it is interesting to note that in the series of experiments just described it failed to grow at 37° C. This led to an attempt by the author to restore the tolerance of this organism to this temperature. Accordingly, cultures of this species were started in 250 cc. Ehrlenmyer flasks containing either potato maltose agar or three per cent Difco Bactopeptone agar or broth. The flasks with the solid medium and those with the liquid nutrient solution were placed at once at 30° C. After the cultures had grown three to four weeks, each series was divided, and one half placed at 32° C., the other half left at 30° C. Simultaneously, transfers were made from the cultures grown at 30° and also placed at 32° C. Each of these cultures grew well. At the end of two months, the procedure was repeated and the cultures which had been growing at 32° were placed at 34°, at which temperature each of the cultures gave excellent growth of the fungus. After the fungus had grown for three months at 34°, transfers were made to fresh media. Some of the cultures were placed at 34°, some at 37°, and one at room temperature. No growth occurred at either 34° or 37° even at the end of two months, but good colonies were produced in the flasks maintained at room temperature. It would appear from this that growth at a temperature of 34° is rather limited and that after a certain time the mycelium loses its ability to grow at the higher temperatures. Also it would seem that the spores, while viable, do not germinate readily, if at all, at 34° C. This is substantiated by preliminary experiments, which showed that although germination of ten weeks old spores took place readily at room temperatures, germination of three and five months old spores is erratic. Only once during these experiments was the writer successful in germinating spores at 37°, and at that time only six per cent germination was obtained. Such erratic results substantiate the work of de Monbreun (2) who also reported difficulty in germinating the aleuriospores. While this appears to be true in cultures that have been maintained over

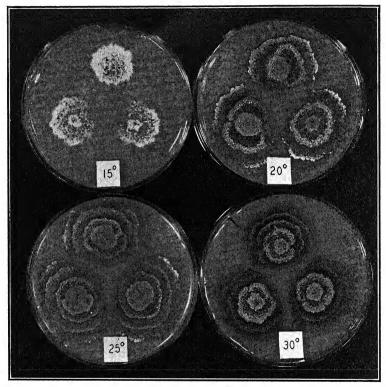


Fig. H. Sepedonium xylogenum Sacc.

a long period of time, nevertheless a more recently isolated strain <sup>4</sup> grew well at 37° C. on this medium. From these experiences it would appear first that the optimum temperature for the growth of the saprophytic phase of *Histoplasma capsulatum* is 25° C. Second, that through more frequent transfers and by growing this organism for longer periods of time at temperatures between 30 and 37° C., or, as shown by Weimer and Harter (5) in the case of

<sup>&</sup>lt;sup>4</sup> This strain was recently isolated from a dog by de Monbreun to whom the writer is deeply indebted for his kindness in supplying the culture.

eleven species of Rhizopus, through the use of different media, it may be possible to restore the tolerance of the saprophytic phase of Histoplasma capsulatum to temperatures as high as 37° C. This supposition has been substantiated in recent work by successfully culturing the fungus (cultures M 250 and M 251) on freshly prepared blood agar at 37° C. In another respect the results of the present studies upon this parasitic fungus in its saprophytic phase are similar to those reported by Moore (4) who stated in his paper on another parasitic organism, Endomyces capsulatus Rewbridge, Dodge and Ayers: "These results seem to indicate that the optimum growth for this organism has been changed from approximately 37.5° C. in its parasitic condition to 25° C. in a saprophytic condition. This latter fact will be demonstrated in the animal inoculation experiments. It also shows that the longer an organism is kept in culture the greater will be its change in physiological phenomena to an optimum point for its changed environment." Histoplasma capsulatum appears to behave much in the same manner, and it is certainly clear that in its physiology as well as its morphology, its saprophytic and parasitic phases are distinct, and that the problem of the change of one phase into the other is in need of intensive study.

#### SUMMARY

The results of the investigations on the effect of temperature on the growth of *Histoplasma capsulatum*, *Sepedonium chrysospermum*, *S. xylogenum* and *Stephanoma tetracoccum* may be summarized as follows:

- 1. The optimum temperature for growth, all factors considered, was 25° C. for H. capsulatum, 20° C. for S. chrysospermum, 25° C. for S. xylogenum, and 20° C. for Stephanoma tetracoccum.
- 2. Sporulation in the case of *Sepedonium chrysospermum*, when grown on potato maltose agar, was greatest, not at temperatures in which maximum radial growth was produced, but at 25° C. Spore production in *Stephanoma tetracoccum*, *Histoplasma capsulatum* and *Sepedonium xylogenum* was correlated directly from the first with the abundance of mycelium. For these forms the optimum temperatures for sporulation were 20° and 25° C. respectively.

3. Attempts to restore the tolerance of *Histoplasma capsulatum* to body temperature (37.5° C.) were only partially successful.

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#### EXPLANATION OF FIGURES

Fig. A. Diagram to show method of measuring colonies; B, graph to show effect of temperature on growth of Sepedonium chrysospermum; C, graph to show effect of temperature on growth of Sepedonium xylogenum; D, graph to show effect of temperature on growth of Histoplasma capsulatum M. 251; E, graph to show effect of temperature on growth of Stephanoma tetracoccum; F, graph to show effect of temperature on growth of Histoplasma capsulatum M. 250.

Fig. G. 1-3. Sepedonium chrysospermum (Bull.) Link showing effect of temperature on growth at end of 8 days on potato maltose agar. 1, colonies at 15° C. show scattered aerial hyphae over the predominantly submerged mycelium; 2, colonies at 20° C. show radiate and rather dense aerial mycelium; 3, colonies at 25° C. show dense, cottony, aerial mycelium and a thin

margin of submerged hyphae.

Fig. H. Sepedonium xylogenum Sacc. showing characteristic colonies after 8 days on potato maltose agar at various temperatures. Note the similar type of growth at all temperatures. Also, that there are zones in which aerial mycelium and aleuriospores are abundant. These alternate with zones in which aerial mycelium and aleuriospores are lacking. The number of zones varies with the temperature.

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## NOTES AND BRIEF ARTICLES

### DODGEA MALENCON

As soon as the description and illustrations of this new genus came to hand, the writer was relatively certain it must be congeneric with *Truncocolumella* Zeller. Therefore, specimens of *T. citrina* Zeller were sent to Malençon to compare with the type of *Dodgea occidentalis* Malençon, and his reply to my inquiry is as follows (translated from French):

"I have examined with interest the specimens of *Truncocolu*mella citrina which recently reached me in excellent condition. To my mind there is no doubt: your genus and mine are absolutely identical. I am entirely in agreement with you on this subject.

"On the other hand it is more difficult for me to say with certainty whether  $Tr.\ citrina$  and  $Dodgea\ occidentalis$  are specifically identical. A priori, I think that they are really the same species but there are certain macro- and microscopic differences between your specimens and Dodge's which permit the existence of some doubt.

"Tr. citrina is two to three times larger than D. occidentalis. Furthermore, your species is a clear yellow while Dodge's specimens were whitish. It is true that the latter had been preserved in alcohol for 17 years, a treatment which might have destroyed their original color. I described the species as whitish, but with reservations concerning the exact original tint, since Dodge furnished me no information on the subject; consequently I qualified my statement on the point (dfr. Bull. Soc. Myc. Fr. 44 (1938): 194. 1939; footnote No. 2).

"The anatomic structure of the two plants is in all respects entirely the same. There is, however, need to note that the spores of  $Tr.\ citrina$  are clearly shorter, more oval, and of more irregular shape than those of  $D.\ occidentalis$ , in which these bodies are long-elliptic, or sometimes subcylindric. . . . Taking into account the differences here described, especially with respect to the size of the carpophores and spores, I believe that it is at present more

prudent to conclude, but only provisionally, that citrina and occidentalis are two distinct but very closely related species. I am equally in accord with you on the subject of the priority of Truncocolumella."

Dodgea Malençon (Bull. Soc. Myc. Fr. 44 (1938): 193–194. 1939) was published March 31, 1939, while Truncocolumella Zeller (Mycologia 31: 6. 1939) was issued February 1, 1939. Dodgea therefore becomes synonymous with Truncocolumella, and for Dodgea occidentalis Malençon a new combination is proposed, namely: Truncocolumella occidentalis (Malençon) Malençon & Zeller comb. nov.—S. M. Zeller.

# **MYCOLOGIA**

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Vol. XXXII November-December, 1940 No. 6

## SOME HETEROBASIDIOMYCETES FROM EASTERN CANADA

G. W. MARTIN

(WITH 9 FIGURES)

Collections made during recent years in the provinces of Ontario and Quebec by Professor H. S. Jackson and students, and by his associate, Dr. R. F. Cain, have brought to light a considerable number of Heterobasidiomycetes. Many of these have been sent to me annually for identification. A selected number, recognized by Professor Jackson as of special interest, were allowed to accumulate and finally sent to me in one lot in the fall of 1939 with the request that they be critically studied and such of them as seemed worthy of record be included in a special paper. The present report is the result of the study of these collections. Among them several seem to be undescribed; others either have not as yet been reported from North America or for other reasons appear to justify discussion and illustration. Of the latter group, only one is here discussed. Since several of the species proposed as new were recognized by Professor Jackson as probably undescribed, he has consented to join me in the authorship of certain of them. The joint authorship is indicated following the specific name in each such case. All the collections mentioned are deposited in the herbarium of the University of Toronto and many of them are also in the collections of the University of Iowa. Unless otherwise stated all collections were made by H. S. Jackson.

[MYCOLOGIA for September-October (32: 575-682) was issued October 1, 1940]

Sebacina (Bourdotia) rimosa Jackson & Martin, sp. nov. (FIG. 1)

Late effusa, floccoso-rimosa, margine indeterminata, ex pallida ad atromelleam; hyphae nodoso-septatae,  $1.5-2~\mu$ , gloeocystidia et basidia gerentes; gloeocystidia clavata, primum hyalina demum flava; probasidiis globosis vel ovatis, usque ad  $16~\mu$  diam., dein cruciato-septatis; basidiosporis subglobosis vel cylindricatis,  $12-13~\times~8.5-9~\mu$ , per repetitionem germinantibus.

Broadly effused, floccose-rimose, with indeterminate margin; pallid to citrine drab (R) \* not greatly altered when soaked; in section 35–70  $\mu$  thick, composed of a thin mycelial layer parallel with the substratum consisting of hyphae 1.5–2  $\mu$  in diameter, with frequent clamp connections, giving rise directly to gloeocystidia and to hyphae which bear both gloeocystidia and basidia; gloeocystidia clavate, often with broad, furcate base, at first colorless, then filled with yellow, amorphous material, 15–35  $\times$  5–7.5  $\mu$ ; probasidia globose or broadly ovate, up to 16  $\mu$  in diameter, becoming longitudinally septate into two or four cells, the cells exhibiting a tendency to separate at the apex; epibasidia rather short, rarely exceeding the hypobasidium, the mature basidia somewhat urniform; basidiospores varying from subglobose to short cylindrical, but mostly broadly ovate, 12–13  $\times$  8.5–9  $\mu$ , germinating by repetition or by the production of a diploid mycelium.

Ontario: Maple, Nov. 13, 1938. On Thuja occidentalis. U. of Tor. 13086. Type.

The lower portion of the hymenium is composed of a nearly continuous layer of colored gloeocystidia; the upper portion of younger, paler, often hyaline gloeocystidia and rather sparsely distributed basidia. Present in every mount are chains of vesicular cells, some filled with homogeneous protoplasm, others empty, but it may be doubted whether these have any connection with the *Sebacina*.

## Sebacina (Bourdotia) Pini Jackson & Martin, sp. nov. (Fig. 2)

Effusa, tenua, margine indistincta, sicca cinerea, humescens ceracea, squalide mellea, in sectione  $50-120~\mu$  cr., gloeocystidia primo pallida, demum flava; probasidiis globosis,  $22-24~\mu$  diam., decentibus cruciato-septatis; epibasidiis brevibus; basidiosporis cylindricatis,  $19-22 \times 9-10~\mu$ , per repetitionem germinantibus.

Effused, thin, arid, with indeterminate margin, smoke gray (R) with pruinose surface when dry, becoming olive buff (R) and

<sup>\* (</sup>R) indicates use of a color name in the sense of Ridgway.

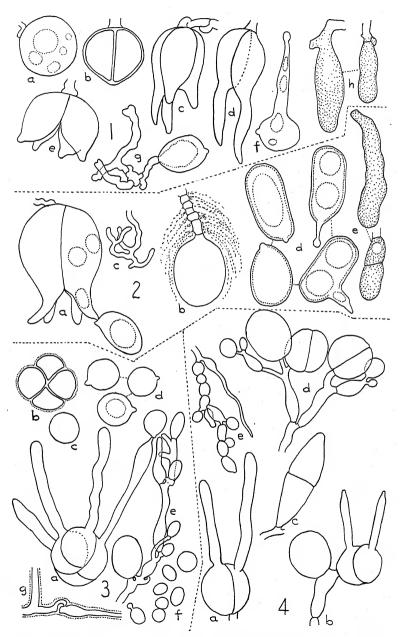


Fig. 1, Sebacina rimosa; 2, S. Pini; 3, Tremella mycophaga; 4, T. simplex.

somewhat waxy when soaked, 50–120  $\mu$  thick; basal layer scantily developed, the bulk of the fructification composed of a dense mass of gloeocystidia and basidium-bearing hyphae; gloeocystidia at first hyaline, then yellow, the contents nearly homogeneous, sometimes divided by a transverse septum into two, rarely three cells,  $15–45 \times 5-6 \,\mu$ ; probasidia borne at the surface at the tips of the fertile branches, broadly obovate, then globose,  $22–24 \,\mu$  in diameter, proliferating from the basal clamp connection, becoming cruciate-septate; epibasidia merged with sterigmata, short, divergent, the mature basidium distinctly urniform; paraphyses colorless, much branched at tips, about  $1 \,\mu$  in diameter; basidiospores mostly cylindrical  $19–22 \times 9–10 \,\mu$  but varying to ovate,  $16–18 \times 10–11 \,\mu$ , germinating by repetition.

Ontario: Maple, Nov. 6, 1938. On *Pinus Strobus*. U. of Tor. 13090. Type.

Differing from all previously described arid, gloeocystidiate species of Sebacina in the very large basidia and spores. There are occasional suggestions of the involucral sheath of collapsed basidia (Fig. 2b) characteristic of many species of Bourdotia but they are not prominent in the present collection. The fungus occurs in rather long and narrow patches on the substratum, the longest being about  $70 \times 5$  mm. It is not unlikely that it may occur in much more extensive growths.

## Tremella mycophaga sp. nov. (FIG. 3)

Pulvinata, molliter gelatinosa, hyalina vel dilutissime rosea aut ochracea, 0.3–1.5 mm. lata; fructificationibus confluentibus, demum subcerebriformibus; conidiis copiosis, hyphis basidioferis portatis, variabilibus, plurimis 4–7  $\times$  2.5–4  $\mu$ ; probasidiis globosis, 13–15  $\mu$  diam., demum cruciatim divisis; basidiosporis globosis, 6–8  $\mu$  diam., per repetitionem germinantibus.

Fructification pulvinate, discoid, 0.3–1.5 mm. in diameter, larger by confluence, up to 1 cm. or more in extent and then covering several adjacent fructifications of the host, soft gelatinous, hyaline to pinkish or pale yellow-brown when wet, horny, hyaline to dark brown (about warm sepia R.) when dry; surface at first smooth but becoming tuberculate-subcerebriform, partly as a result of confluence, partly by the formation of small tubercles on the individual units; internal hyphae immersed in a soft jelly, slender but irregular, with many vesicular swellings and abundant and conspicuous clamp connections; conidia profuse at all stages, variable in size and shape but mostly subglobose,  $(2-)4-5(-7) \mu$  in diameter, or

ovate,  $4-7 \times 2.5-4~\mu$ , germinating by budding; basidia borne on same hyphae as conidia; probasidia globose,  $13-15~\mu$  in diameter, readily detached, becoming cruciate-septate; epibasidia up to  $50~\mu$  in length,  $2-3~\mu$  in diameter except toward the tip where they swell to  $4-6~\mu$ , forming conspicuous apophyses below the slender sterigmata; basidiospores  $6-8~\mu$  in diameter, germinating by repetition.

On Aleurodiscus amorphus on Abies balsamea: Ontario, Quebec, New York.

Specimens examined: Ontario: Algonquin Park, Sept. 18, 1938, U. of Tor. 13421. Type; Sept. 15, 1938. U. of Tor. 13420; Sept. 18, 1930, U. of Tor. 13448; Lake Temagami, June 21, 1933, U. of Tor. 6399; July 20, 1935, U. of Tor. 8342; Aug. 19, 1936, U. of Tor. 11063; Aug. 29, 1936, U. of Tor. 11060; Aug. 20, 1937, U. of Tor. 13547. Quebec: Ste. Catharine, Aug. 25, 1938, R. F. Cain 11124; Duchesnay, Aug. 25, 1938.

In connection with his study of Aleurodiscus amorphus, Stork (Am. Jour. Bot. 7: 447–448. 1920) described and illustrated, but did not name this species. Stork's description was apparently drawn largely from stained microtome sections and was, of course, incidental to the subject matter of his paper. He did note the tendency of the hypobasidial segments to separate. From the study of the Canadian material it seems certain that the segments may become completely separate and round up in spore-like form (FIG. 3b, c) before developing epibasidia, in which case they can be distinguished from basidiospores only by the absence of an apiculus. Dr. Stork has kindly placed his slides at my disposal and there can be no question that his reference is to the present species.

## Tremella simplex Jackson & Martin, sp. nov. (FIG. 4)

Pulvinata, molliter gelatinosa, hyalina vel dilutissime rosea aut ochracea, 0.3–1.5 mm. lata; fructificationibus confluentibus, demum subcerebriformibus; conidiis copiosis, hyphis basidioferis portatis, variabilibus, plerumque 4–7  $\times$  2.5–4  $\mu$ ; probasidiis subglobosis, 10–13  $\mu$  diam.; vel fusoidiis et igitur pro portione gracilis, uniseptatis, ex hyphis haud nodosis; basidiosporis subglobosis, 6.5–8  $\mu$  diam.

Exactly like T. mycophaga in habit, shape, size, color and consistency, and like it, bearing conidia on the same branches as the basidia; differing in the complete lack of clamp connections, the smaller probasidia varying in shape from globose through ellip-

tical to elongate fusoid; in the constantly single septum which, in the shorter basidia may be in any plane with reference to the axis of the basidium, but is usually transverse or nearly so in the longer basidia. The spores are not quite so regularly globose as in T. mycophaga but the difference is not great enough to be stressed.

On Aleurodiscus sp. on Thuja occidentalis, Ontario and Quebec. Specimens examined: Ontario: Lake Temagami, Sept. 4, 1937, U. of Tor. 11650, Type. Same locality, Aug. 13, 1937, U. of Tor. 11653A. Quebec: Ste. Catharine, Aug. 25, 1938.

There is a strong temptation to regard this as a haploid variety of  $T.\ mycophaga$ . The lack of clamp connections and the constant 2-celled character of the mature basidia together with their smaller size and tendency to greater irregularity of shape and orientation of the septum are exactly what might be expected of a haploid form. Whether this is the case or not can be decided, however, only by cultural studies and cytological comparison. In the meantime the existence of three collections from two rather widely separated localities, all parasitizing an undescribed species of Aleuro-discus, which is not the host of  $T.\ mycophaga$ , justify designating this form by a distinct name.

PLATYGLOEA PENIOPHORAE Bourd. & Galz. Bull. Soc. Myc. Fr. 25: 17. 1909 (Fig. 5)

A collection on *Tilia* near Maple, Ontario, Oct. 6, 1937 (U. of Tor. 12401), is doubtfully assigned to this species. Another on *Populus*, from Holland River Marsh, May 6, 1936, by R. F. Cain (U. of Tor. 12834) is certainly the same. The former is marked "associated with *Peniophora* sp." but aside from some large spores, clearly not belonging to the *Platygloea*, and some mycelial fragments, there is little that suggests *Peniophora* in the mounts. Nevertheless, I believe that it is preferable to refer these collections to Bourdot and Galzin's species for the time being rather than to give them a new name.

In the original description no spore size is given. Later Bourdot and Maire (Bull. Soc. Myc. Fr. 36: 69. 1920) reported them as  $7-10 \times 4-6 \mu$ . Wakefield and Pearson (Trans. British Myc. Soc. 8: 219. 1923) give the measurements as  $8-9 \times 5-5.5 \mu$  and note

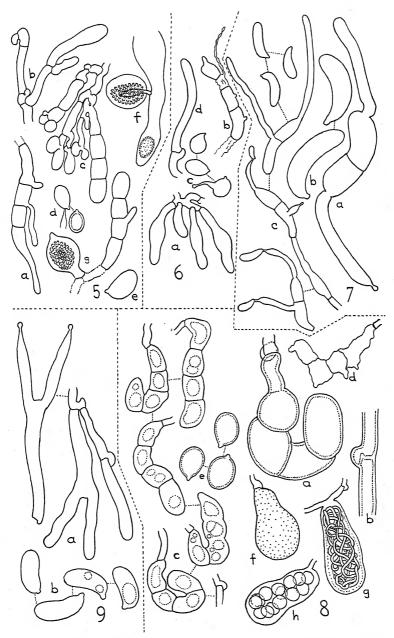


Fig. 5, Platygloca Peniophorae; 6, P. fusco-atra; 7, P. pustulata; 8, Helico-basidium candidum; 9, Ceracea canadensis.

that they germinate by repetition. In their final publication Bourdot and Galzin (Hym. France 12. 1928) cite the spore size as  $7-8 \times 5-6 \,\mu$ . There are other differences between the various descriptions. Bourdot and Galzin emphasize the horny character when dry. Wakefield and Pearson describe the fungus as not horny but thin, white and markedly pulverulent, with shorter "sterigmata." They attribute the differences, reasonably enough, to the fact that their material was probably younger.

The Canadian collections form rather conspicuous effused white or ochraceous patches over 10 cm. long and 2 cm. wide. The presence of thicker patches, somewhat gelatinous when wet, suggests that the fructifications originate as separate pustules which rather quickly anastomose. A few horny patches are present, but these are either sterile or the Platygloea may be growing over the surface of some other fungus, since in both collections the wood is old and rotten, and remnants of various other fungi are present. delicate tortuous hyphae are well provided with clamp connections and there is a clamp connection at the base of each basidium, which proliferates to form another basidium, so that the groups of basidia tend to occur in loose, one-sided, cymose clusters. Some of the basidia in such clusters fail to develop fully and become transformed into conidiophores which produce irregularly globose, nearly sessile conidia. The basidiospores are ovate, very slightly flattened ventrally and with a small, or rarely large apiculus, mostly 5-7  $\times$  3.5–4.5  $\mu$ , but occasionally as large as 8.5  $\times$  5  $\mu$ .

In addition to these structures there are present in abundance on both collections curious vesicular cells, borne upon hyphae with clamp connections and sometimes interspersed with the basidia. The contents are at first homogeneous but soon become nearly filled with small oval bodies, about  $1.5 \times 1~\mu$ . In some cases these seem to surround a central, columella-like stalk. These are perhaps the subfusoid bodies mentioned in Bourdot and Galzin's first description. I am inclined to interpret them as galls caused by a parasitic fungus. Dr. F. K. Sparrow, to whom the sketches were submitted, suggested that they might possibly represent a *Woronina* parasitic on the *Platygloea*.

## Platygloea fusco-atra Jackson & Martin, sp. nov. (FIG. 6)

Pustulata, gelatinosa, confluens, humescens brunneo-ochracea, sicca fuscobadia; basidiis cylindraceis,  $22-25 \times 2.5-3.5 \,\mu$ , transverse 3-septatis; paraphysibus cylindraceis,  $2\,\mu$  cr.; basidiosporis ovatis vel lachrymatis, 5.5-6  $\times$  4-4.5  $\mu$ , per repetitionem germinantibus.

Pustulate, the pustules circular, 0.5–1.5 mm. in diameter, then anastomosing in reticulate fashion, soft waxy-gelatinous, yellow-brown when moist, becoming dark reddish brown or blackish and horny when dry; paraphyses cylindrical,  $25-30\times2~\mu$ , each with a prominent clamp connection at base; probasidia cylindrical-clavate, often ventrally swollen, then cylindrical,  $22-25\times2.5-3.5~\mu$ , becoming transversely 3-septate, each cell developing a rather long epibasidium; basidiospores oval or tear-shaped,  $5.5-6\times4-4.5~\mu$ , germinating by repetition.

Ontario: Aurora, Oct. 30, 1937, on decayed wood of *Tsuga canadensis*, U. of Tor. 13552. Type.

The dark color, the reticulate pattern and the small basidia accompanied by the coarse paraphyses with the prominent clamp connections should make this species easy of recognition.

## Platygloea pustulata Martin & Cain, sp. nov. (FIG. 7)

Gelatinosa, pustulata, 1–3 mm. diam., humescens alba, sicca cornea, inconspicua; hyphis hyalinis, tenuibus; hypobasidiis cylindratoclavatis, demum transverse uniseptatis; epibasidiis cylindratis, elongatis, 3  $\mu$  diam.; basidiosporis cylindratis, curvulis,  $20-22 \times 5-6 \mu$ .

Gelatinous, pustulate, 1–3 mm. in diameter, becoming larger by confluence, pure white varying to dingy white or grayish when soaked, drying to an inconspicuous horny film; in section composed of radiating, branched hyphae, some of the branches becoming slender, branched paraphyses 2–2.5  $\mu$  in diameter, others swollen at the tips, the swellings either proliferating or developing into cylindrical-clavate probasidia mostly 30–35  $\times$  6–7  $\mu$ , these becoming transversely 1-septate, each cell sending out a cylindrical epibasidium variable in length but usually rather long and 2–3  $\mu$  in diameter except just below the sterigma where it is often somewhat enlarged; basidiospores cylindrical-allantoid, often strongly curved, (16–)20–22  $\times$  (4–)5–6  $\mu$ .

Quebec: Duchesnay, Aug. 24, 1938, on bark of *Abies balsamea*. Type.

Ontario: Lake Temagami, Aug. 10, 1939, on coniferous wood, R. F. Cain (U. of Tor. 14977); Algonquin Park, Sept. 9, 1939, on bark of *Abies balsamea*, R. F. Cain (U. of Tor. 14978).

Differing from previously known species of Platygloea in the 2-celled basidia and the slender, often strongly curved basidiospores. The empty hyphae below many of the basidia are more or less swollen in such a way as to suggest the empty probasidia of Jola (FIG. 7c, center). These are not always present, however, and there may occasionally be two of them. It seems evident that a basidium may start to form when the fructification is beginning to dry and then, when a rain causes the jelly to swell, it proliferates, forming a new basidium near the new surface. Möller (Protobasidiomyceten, pl. 4, Fig. 5b) shows a similar empty hypha under a basidium of *P. blastomyces*. In the present species the empty walls of the old vesicle frequently surround the proliferation, much as the old walls of an emptied sporangium in Saprolegnia surround the new sporangium. In the mounts, numerous basidia are completely detached from their basal hyphae and it seems probable that they may readily be detached in nature when the basidiocarp swells. This is borne out by the way in which some of such detached basidia bear the epibasidia at the basal and distal ends (FIG. 7a). The regular alternation of protoplasm and vacuoles in the paraphyses gives these structures a characteristic and striking appearance, especially under a low power objective.

## Helicobasidium candidum sp. nov. (FIG. 8)

Resupinatum, maculiforme dein effusum, tenue, arcte adhaerens, immarginatum, album, subfarinaceum; contexto laxo ex hyphis nodosis,  $2-3~\mu$  cr. compositis; basidiis clavatis, saepius curvatis vel varie flexis, quadricellularibus,  $60-65 \times 12-13~\mu$ ; sporis ovatis,  $18-20 \times 14-15~\mu$ .

Resupinate, pure white, at first floccose, then expanding and anastomosing, finally broadly effused, thin, arid, with indeterminate arachnoid margin, the older portions very faintly yellowish when soaked; in section up to  $250\,\mu$  thick at center, thinning to a mere subiculum at margins; basidial layer originating under epidermis and erumpent from lenticels, covered by a loosely woven pseudotissue of gelatinous hyphae, mostly 2–3  $\mu$  in diameter, with clamp connections at many of the septa; surface sterile; basidia at first broadly ovate, then cylindrical, straight or tortuous to strongly

recurved, becoming 4-celled by the formation of transverse septa,  $60\text{--}65 \times 12\text{--}13~\mu$ ; basidiospores broadly ovate, somewhat flattened ventrally,  $18\text{--}20 \times 14\text{--}15~\mu$ . Germination not observed.

QUEBEC: Duchesnay, Aug. 26, 1938, on dead branches of standing *Acer*. Type.

Apparently closest to H. farinaceum Höhnel, but differing in its nearly pure white color, much larger basidia, the somewhat longer and much thicker spores and the numerous clamp connections.

The surface of the fructification is sterile, bearing a very few old, emptied basidia (Fig. 8d), while the numerous young basidia are developing in a basal layer, suggesting that after an early fruiting stage the fungus was preparing for a second fruiting period when collected. Very few spores were seen and none of these were attached, so it is by no means certain that those associated with the fungus really belong to it. On the other hand, the species is so distinctive that it seems justifiable to name it.

The huge, septate basidia suggest the spores of *Delortia*, which Patouillard (Bull. Soc. Myc. Fr. 4: 43. 1888) at first grouped with the Auriculariaceae, later (Tax. Hymen. 33: 1900) removing it to the Hyphomycetes, a decision confirmed by Linder (Ann. Missouri Bot. Gard. 16: 338. 1929). At the base of each basidium is a slender stalk cell, apparently derived from the original probasidium, since the clamp connection is borne at its base (Fig. 8a).

Large clavate or obpyriform bodies are associated with the fructification and at first suggest cystidia. Their occurrence is too irregular, however, to make this seem possible. Some have homogeneous contents (Fig. 8f), others are filled with a tangle of hyphae (Fig. 8g) and still others with rather irregular, globose, spore-like bodies (Fig. 8h). I believe they are galls of a parasitic fungus similar to those observed on *Platygloea Peniophorae* but certainly not the same.

## Ceracea canadensis Jackson & Martin, sp. nov. (FIG. 9)

Effusa, ceracea, adnata, tenuis, laevis, ex lutea aurantiaca, ambitu albo floccoso; hyphis 2.5–3.5  $\mu$ , copiose nodulosis; probasidiis anguste clavatis,  $30-33\times3.5-4~\mu$ ; epibasidiis,  $20-30\times2.5~\mu$ ; basidiosporis hyalinis, cylindraceis, rectis vel subarcuatis, haud septatis,  $11-13.5\times4.5-5~\mu$ .

Effused in small patches, the largest  $30 \times 8$  mm., deep chrome (R) in older portions, fading to light orange (R) toward the margin; margin white, floccose; surface pulverulent, cracking, becoming waxy when soaked but not gelatinous; in section 175-200 u thick, consisting of a loosely interwoven basal portion arising directly from the substratum, composed of erect, branching hyphae 2.5-3.5 u in diameter bearing numerous clamp connections, supporting a dense hymenium, 45-50  $\mu$  thick, mainly of basidia, but including a few cylindrical, paraphysis-like filaments  $2-3 \mu$  in diameter, arising from the same branches as the basidia; probasidia, at maturity, mostly  $30-33 \times 3.5-4 \mu$ , giving rise to two rather long epibasidia 20-30 μ long and 2.5 μ in diameter; basidiospores cylindrical straight or curved, unseptate, with prominent apiculus, 11- $13.5 \times 4.5-5 \mu$ ; germination not observed.

ONTARIO: Port Alexander, Sept. 13, 1939, on coniferous wood (U. of Tor. 14103), Type; Algonquin Park, Sept. 11, 1939, on conifer. R. F. Cain (U. of Tor. 14976).

Brasfield (Lloydia 3: 106-108. 1940.) has concluded that Ceracea is a valid genus. The present species seems clearly distinct from any of the few species previously recognized.

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#### EXPLANATION OF FIGURES

Except where otherwise noted, all figures drawn with aid of camera lucida at a magnification of  $\times$  2400 and reduced in reproduction to approximately  $\times$  1000.

Fig. 1. Sebacina rimosa. a, probasidium; b, septate, thick-walled hypobasidium; c, 4-celled basidium; d, 2-celled basidium; e, 4-celled basidium with segments separating; f, basidiospore germinating by repetition; g, basidiospore germinating to form mycelium with clamp connections; h, two gloeocystidia.

Fig. 2. Sebacina Pini. a, mature 4-celled basidium with young basidiospore; b, probasidium with involucral sheath presumably formed of gelatinized walls of spent basidia; c, tip of paraphysis; d, four basidiospores, two germinating by repetition; e, two gloeocystidia, the lower one septate.

Fig. 3. Tremella mycophaga. a, typical detached basidium; b, septate, thick-walled hypobasidium, the segments ready to separate; c, basidiosporelike body apparently derived from segment of such a basidium as preceding; d, three basidiospores; e, hypha with clamp connections bearing probasidium and conidia; f, seven detached conidia, one germinating by budding; g, internal hypha with clamp connection.

Fig. 4. Tremella simplex. a, typical basidium; b, probasidium and small basidium; c, fusiform, transversely septate hypobasidium; d, hypha bearing both basidia and conidia; e, conidia.

- Fig. 5. Platygloea Peniophorae. a, basidium; b, young probasidium and crozier-like hyphal tip; c, cluster of conidiophores with basidium; d, young basidiospore and old, thick-walled basidiospore; c, unusually large basidiospore; f, swollen hypha with parasitic thallus near tip, and lateral gall with columellate axis; g, gall at base of basidium.
- Fig. 6. Platygloca fusco-atra. a, cluster of young basidia; b, mature basidium; c, three spores, one germinating by repetition; d, paraphysis.
- Fig. 7. Platygloca pustulata. a, detached basidium developing epibasidia at either end; b, two basidiospores; c, three basidia, two detached and three basidiospores. c,  $\times$  460.
- Fig. 8. Helicobasidium candidum. a, basidium; b, clamp connection; c, five basidia and clamp connection; d, spent basidium; e, three basidiospores; f, parasite, early homogeneous stage; g, same, intermediate stage; h, same, late stage. e to h inclusive, e 460.
- Fig. 9. Ceracea canadensis. a, two basidia and paraphysis; b, four basidiospores.

## STUDIES IN THE GASTEROMYCETES. I. THE GENUS DICTYOCEPHALOS

### W. H. LONG AND O. A. PLUNKETT

(WITH 13 FIGURES)

This paper discusses the taxonomic position of *Dictyocephalos*, lists its synonyms, gives an emended description of genus and species, and records new data on its occurrence and distribution.

The family Tylostomataceae as defined by Cunningham (1932) contains those genera which have a sporocarp elevated at maturity upon a definite elongated stem, the walls composed of two layers, the exoperidium and the endoperidium, and the gleba consisting of spores and a well developed capillitium (with one exception). Six genera were placed by Cunningham in this family as follows: Battarrea, Chlamydopus, Phellorina, Podaxon, Queletia and Tylostoma. The genera Dictyocephalos and Schizostoma should be added since they have all the characters assigned to this family. The following synopsis shows the relationship existing between Dictyocephalos and the other genera in the family.

#### KEY TO THE FAMILY TYLOSTOMATACEAE

## (adapted from Cunningham)

1	Basidia in fasciculate clusters, persistent at maturity
	Basidia not fasciculate, disappearing at maturity
	Sporocarp traversed by an axile columella
2.	Sporocarp carried at apex of stem, columella none 4
4.	Exoperidium continuous with stem, endoperidium a cupulate extension
	of the stem apex
4.	Exporidium not continuous with the stem, sporocarp seated on the
	truncate expanded stem apex, stem volvate 5
5.	Gleba not cellular, dehiscence by an apical stomaChlamydopus.
5.	Gleba cellular, dehiscence by the irregular breaking away of the
	peridium
3.	Elaters present in the gleba
3.	Elaters not present in the gleba 6
б.	Sporocarp with a definite apical stoma
б.	Sporocarp dehiscing irregularly
6.	Sporocarp dehiscing by irregular stellate rays

The genus *Dictyocephalos* was erected by Underwood (1901) on specimens collected by E. Bethel in Colorado in 1897.

Dictyocephalos Underwood, Bull. Torrey Club 28: 441. 1901.

Battareopsis P. Henn. Hedwigia Beibl. 41: 212. 1902.

Whetstonia Lloyd, Myc. Writ. 2: 259. 1906.

Sporophore hypogeous, enclosed in a volva during early stages of growth, erumpent as maturity approaches; stipitate, stem stout, solid, becoming woody; peridium of two layers, outer (exoperidium) roughened, inner (endoperidium) coriaceous to membranaceous, seated on the expanded discoid apex of the stipe; dehiscence by the irregular breaking away of the peridium; gleba powdery, having permanent cells, spores, and persistent fascicles of basidia, true capillitium none; spores globose to subglobose, fulvous, verrucose.

HABITAT: Growing solitary or in groups of 2–5 individuals, in sandy or adobe alkaline soil, in arid or semi-arid regions.

Type Species: Battarrea attenuata Peck. Distribution: North America; Africa.

## Dictyocephalos attenuatus (Peck) comb. nov.

Battarrea attenuata Peck, Bull. Torrey Club 22: 208. 1895. Dictyocephalos curvatus Underwood, Bull. Torrey Club 28: 441. 1901.

Battarcopsis Artini P. Henn. Hedwigia Beibl. 41: 212. 1902. Whetstonia strobiliformis Lloyd, Myc. Writ. 2: 259. 1906. Phellorina strobilina as shown by Lloyd, Myc. Writ. 5: 735. 1917.

Sporophore 7 to 56 cm. tall, originating 4 to 20 cm. below the surface of the soil, often with 1–2 white cord-like roots; sporocarp globose to subglobose, depressed, often irregular, 2–6 cm. high by 5–13 cm. broad, seated on the discoid apex of the stipe, basal portion hard, thick, with the narrow margin usually concave beneath; the discoid apex, when freed of gleba light tan to white, convex and coarsely reticulate by the boundary walls of broad shallow pits (Fig. 1); exoperidium fleshy to gelatinous when young, developing horny to subcartilagenous scales with age which may be small and more or less persistent (Figs. 4, 9), or large 4–5 sided pyramidal warts (Fig. 2) 1–2 cm. broad by 1–1.5 cm. tall, normally deciduous,

leaving a decided scar on the endoperidium (FIG. 6); endoperidium 1–2 mm. thick, basal portion often coriaceous and persistent, upper part membranous, brittle when dessicated, dehiscing by breaking into irregular pieces which soon fall away leaving the gleba exposed (FIGS. 3, 10); stipe curved, sometimes straight, 5–52 cm. tall,

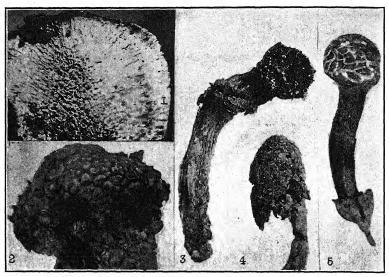


Fig. 1. The white reticulate-pitted upper surface of the discoid apex of stem. California plant, 1936 crop,  $\times$  9/10. 2, large pyramidal warts of exoperidium. California plant, 1938 crop,  $\times$  5/8. 3, sporophore with naked cellular gleba and coarse annulus, New Mexico plant,  $\times$  2/5. 4, coarse veil and the small scales of the exoperidium, New Mexico plant,  $\times$  3/7. 5, plant with radicating base, cupulate volva and brown flakes of exoperidium on the whitish endoperidium, California plant, 1939 crop,  $\times$  3/8.

2–5 cm. thick at top, 1–4 cm. at bottom, solid (except where hollowed out by insects), terete, or flattened, often deeply sulcate, usually attenuate below, subfleshy, drying subcoriaceous to woody, context when young, white becoming walnut brown to vandyke brown with age,¹ outer surface uneven and peeling, often with coarse, spreading or reflexed scales (FIGS. 6, 8) caused by the outer layers of the stipe cracking both transversely and longitudinally from weathering, base of stipe often pointed and becoming entirely free from the enclosing volva (FIG. 7); volva persistent, usually cupulate (FIG. 5) to obconic, sometimes tubular, laciniate-incised, 3–11 cm. tall by 4–8 cm. wide at top, walls 2–4 mm. thick,

<sup>&</sup>lt;sup>1</sup> Ridgway, R. Color standards and color nomenclature, p. 1-111 plus 1-43, 1912.

rupturing from 2-8 cm. below surface of soil, thereby exposing the ascending sporocarp to the dirt for this distance during elongation, walls apparently composed of three layers, inner layer a thin tissue which deliquesces into a blackish fluid just preceding and during elongation, median layer semigelatinous when young, becoming horny with age, outer layer white to tan, hard, chalky in texture; gleba foetid, with odor of decaying fish, pecan brown to mikado brown (after Ridgway), cellular (FIG. 10), cell wall white, fragile, membranous, composed of a hyaline amorphous central tissue overlaid by a dense network of branching colorless to fulvous hyphae, easily fragmenting and falling away in laciniate irregular flakes and shreds, cell walls in bottom of the gleba thicker, firmer and more permanent, often persisting as broad, flattened, pointed teeth on the exposed convex surface of the glebal floor long after the gleba has disappeared; capillitium, free capillitium absent, but the hyphae composing the outer layers of the glebal cell walls may break loose and simulate capillitial threads; spores globose to subglobose, 5-7 microns, walls thin, fulvous, verrucose; basidia clustered bearing 1-4 spores on short sterigmata.

Type locality: Nevada, United States of America.

#### DISTRIBUTION AND SPECIMENS

#### AFRICA:

EGYPT. Alexandria, in Villa des Tito: Artin-Pascha-Jacub, Dec. 1901. 1 specimen in Berlin Mus., Type of Battareopsis Artini P. Henn.

Southwestern Morocco. Goulimine, 1936. 1 specimen in Herb. Lab. Crypt. Mus. Nat. d'Hist. Nat. Paris, France, under name Dictyocephalos curvatus.

SOUTHERN RHODESIA. Wankie District (county), Wankie, elev. 2448 ft., Albert Giese, 1916, comm. Miss A. V. Duthie. 1 specimen (½ plant) in Lloyd Myc. Coll., Washington, D. C., under name Phellorina strobilina. The other half of this plant is in the Nat. Mus. of Southern Rhodesia at Bulawayo.

#### NORTH AMERICA:

NEVADA. C. W. Irish, comm. Dr. Thomas Taylor, 1895. 1 specimen in New York State Mus., Albany, Type of Battarrea attenuata Peck.

Colorado. Grand Co. Colorow, 4 miles south of Kremmling, elev. 7800 ft., E. Bethel, August, 1897; several plants (at

least 3) in New York Bot. Garden, Type of Dictyocephalos curvatus Underwood; 3 plants (fragments) in Myc. Coll. Bureau Plant Industry, Washington, D. C., Reliquiae Bethelianae, Ex type collection of D. curvatus; 1 plant in Lloyd Myc. Coll. (5634), E. Bethel, 1897, part of type collection; a pinch of gleba and a prepared microscopic mount in Lloyd Myc. Coll. (98829), taken by Lloyd from Type at New York Bot. Garden. All under name of D. curvatus.

MINNESOTA (?). Comm. Dr. Mary S. Whetstone, 1906. 1 specimen (½ plant) in Lloyd Myc. Coll., Type of Whetstonia strobiliformis Lloyd. The other half of this type specimen is in the Patouillard Herb. at the Farlow Herb. (1324).

New Mexico. Sandoval Co., 5 miles west of San Ysidro, on State Highway 44, elev. 6200 ft., W. H. Long, Oct. 25 and Nov. 1, 1927. 3 plants in Long Herb. (8053 & 8054).

California. Los Angeles Co., 5 miles east and 2½ miles north of Lancaster, elev. 2350 ft., O. A. Plunkett & W. H. Long, June 1, 1938; 75 plants in Long Herb. (8230); O. A. Plunkett, Sept. 9, 1938; 17 plants in Long Herb. (8231) and Oct. 5, 1938; 50 plants, of which 18 are in Long Herb. (8344), 28 in Plunkett Herb. at Los Angeles, and 4 plants in Herb. of Herbert Granquist, Lancaster, Calif., W. H. Long, August 24–27, 1939; 987 plants of which 985 are in Long Herb. (8436 & 8437) and 2 plants in Herb. of Paul & Marion Rea (210), Santa Barbara, California. The above distribution of Dictyocephalos shows a range in altitude from near sea level at Alexandria, Egypt, to 7800 feet in Colorado.

#### THE SYNONYMY OF DICTYOCEPHALOS ATTENUATUS

Battarrea attenuata Peck. The original description of this species agrees in every particular with our plant even to the number of individuals found in the tufts and also in the strong foetid odor of the gleba. Peck's description was made from a single old dried plant and from notes furnished by the collector. The type specimen should be in the New York State Museum but it has been misplaced.

This plant does not belong to the genus Battarrea, as now de-

fined, but does agree in all essential characters with *Dictyocephalos*. It is therefore transferred to this genus as *Dictyocephalos attenuatus*.

Dictyocephalos curvatus Underwood. An examination of a part of the type collection shows that our plants are identical with it. The species name, D. curvatus, can not be retained since it is antedated six years by Peck's Battarrea attenuata.

Battareopsis Artini P. Henn. The writers have not examined this material but the original description, and the illustrations of the plant by Lloyd (1898–1925), agree fully with Dictyocephalos attenuatus; it has the cellular gleba, the reticulate discoid apex of the stipe, woody stem, horny volva, persistent fascicles of basidia and the same type of spores. Nothing is known of the peridium or method of dehiscence, since these characters were destroyed when the plant emerged.

Whetstonia strobiliformis Lloyd. The senior author examined the type in the Lloyd Myc. Coll. and found that it had all the characters of *D. attenuata* even to the peculiar structure of the walls of the glebal cells. The specimen is unusual in having a stipe with a bulbous base; three of the California plants have bulbous bases similar to the Minnesota specimen.

Phellorina strobilina in part: while studying the specimens listed as Phellorina in the Lloyd Myc. Coll., the senior writer found one plant which did not belong to this genus. It had the following legend; "Cat. No. 30315 Lloyd Collection, Phellorina strobilina, Stellenbosch, S. Africa, Coll. Miss A. V. Duthie, det. C. G. Lloyd." The specimen has the typical cellular gleba, same structure of the glebal cell walls and all other characters of Dictyocephalos attenuatus. The sporocarp is 6 cm. broad by 4 cm. high, covered with pyramidal warts, and is seated on the expanded discoid apex of the stipe. The plant does not have the urceolate extension of the apex of the stem nor the exoperidium continuous with the exterior of the stipe as is the case in the genus Phellorina. This is the plant that Lloyd shows in his Myc. Writ. 5: 735, f. 1101 under name Phellorina strobilina.

The photograph of the type of *Phellorina strobilina* (Kalch.) as shown by Lloyd in his Myc. Writ. 1: pl. 27, f. 3 is very similar in general appearance to *Dictyocephalos attenuatus* and might well

be this plant if the gleba were cellular, in which case the species name of our plant would have to be changed to *Dictyocephalos strobilinus* (Kalch.).

## DISCUSSION AND HISTORY OF THE VARIOUS COLLECTIONS

The Egyptian plant, Battareopsis Artini, was collected at Alexandria, Egypt, growing under an asphalt pavement 2 cm. thick, on

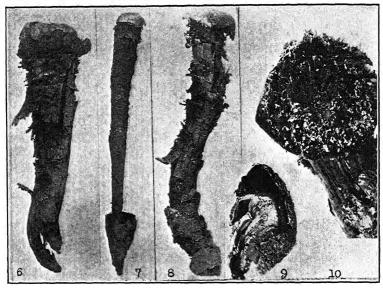


Fig. 6. Scars on endoperidium where the warts of exoperidium peeled off, also shows the rough scales on stipe. California plant, 1937 crop,  $\times$  1/3. 7, a slender very attenuate plant with a pointed stipe free from the obconic volva. California plant, 1935 crop,  $\times$  1/3. 8, a curved sporophore with a scaly stipe and knob at base where volva was attached. California plant, 1937 crop,  $\times$  1/3. 9, longisection view showing the overhanging margin of the pileus and the small scales of the exoperidium. New Mexico plant (reverse side of figure 4),  $\times$  3/7. 10, gleba showing the permanent cells with membranous walls. New Mexico plant,  $\times$  1.

emerging it cracked the asphalt for a radius of 50 cm. around the plant. This specimen apparently reached Berlin in 3 separate pieces, the volva, stem and cap as shown by Lloyd, Myc. Writ. 1: pl. 22. The volva on this plate (Fig. 2) is tubular and not flaring as illustrated by Hennings (1902) in Hedwigia page 213; also the stipe in this drawing is apparently reversed as to position,

the small end should be inside the volva and the large end attached to the cap, since the plant was probably attenuate toward the base, as is usual in this species.

The Moroccan plant, *Dictyocephalos curvatus*, as figured and discussed by Malençon (1935–1936), was discovered by a native collector in the environs of Goulimine in the southwestern part of French Morocco, to the north of the province of Rio de Oro. Only one plant, an old deformed one, was found growing in alkaline soil in a hot semi-desert region. The stipe was bent near the top with the sporocarp split into three distinct heads or lobes, each lobe bearing some gleba. Similar plants with 2- to 4-lobed sporocarps are present in the California collections. This Moroccan plant is undoubtedly *Dictyocephalos attenuatus*.

The Rhodesian specimen, called by Lloyd *Phellorina strobilina*. Dr. G. Arnold, Director of the National Museum of Southern Rhodesia at Bulawayo, says in a recent letter that this specimen was collected on a road near or in Wankie which is situated on the line from Bulawayo to Victoria Falls about Lat. 18° S. and Long. 27° E. in the geological formation known as the Karroo System.

The Nevada material, *Battarrea attenuata* Peck, was found commonly growing in tufts of 3 to 5 individuals in dry sandy soil. The plants were almost wholly buried in the ground, appearing above the surface only in seasons after heavy snow-falls had melted gradually and moistened the earth deeply. The locality in Nevada where the plants were found is not recorded.

The Colorado plants were found by Bethel in an arid region in the northwestern part of Colorado growing in soft, alkaline adobe soil, destitute of any other vegetation. Some plants were entirely out of the ground while others were standing about one inch deep in the soil. Some had stems much bent, others were twisted like a corkscrew with portions of the stalk split and bent back. Bethel found fragmentary remains of this species quite abundantly in many places on arid mesas of western Colorado near the Utah line.

The Minnesota specimen, Whetstonia strobiliformis Lloyd. Only one plant was found and it probably was not collected in Minnesota, but from some place farther south in an arid or semi-arid country since all other known collections have been found in

such regions. The senior writer tried to learn the actual source of the Minnesota plant but without success.

The cavities in the stem of this specimen were caused by insects as evidenced by the dark brown frass still present. The overhanging margin at the base of the exoperidium is very similar to

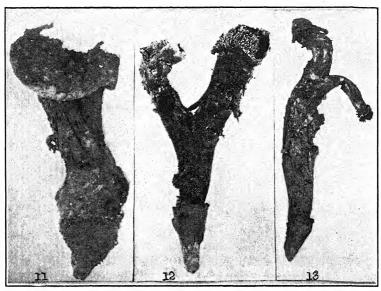


Fig. 11. A sporophore destitute of a true volva, only a mass of dirt held together by mycelial hyphae at base of stipe. California plant, 1938 crop,  $\times$  1/2. 12, a forked plant with radicating base and obconic volva. California plant, 1936 crop,  $\times$  1/4. 13, a large plant with one side branch and the stub of a second branch below the first one. California plant, 1938 crop,  $\times$  1/3.

that on one of the New Mexico plants (FIGS. 4, 9). Lloyd gives some good illustrations of this plant in Myc. Writ. 2: pl. 90, f. 1–5. The specimen in the Lloyd Myc. Coll. does not have a volva and the base of the stipe indicates that if one were present when young it was not very pronounced. Two similar plants, without any signs of volvas (FIG. 11), were found in the California material, although companions in the same collections have well developed volvas.

The New Mexico specimens. The three plants of this collection were fresh, having just emerged when found. They were grow-

ing in an open unshaded area at the lower end of a long shallow wash in the alkaline soil deposited by the water, 100 yards outside of the eastern boundary of the Ojo del Espiritu Santo Grant on state Highway 44.

The plants differ considerably as the following data show. The larger one has an irregular, thin, brittle, erect collar around the base of the exposed gleba; a rough lacerate annulus 2-4 cm. below the sporocarp, consisting of pieces of the peridium and the outer layers of the stem which tore loose during elongation (FIG. 3); the scales of the exoperidium are large coarse warts 10-15 mm. wide by 3-5 mm. high. The second plant does not have either a collar or an annulus, but has a wide overhanging margin at base of pileus with remnants of the torn walls of the stipe and of the peridium forming a coarse veil (FIG. 4); scales of exoperidium thin, small, 3-5 mm. across. The third plant is stout, deformed and split lengthwise just below the sporocarp with the outer layers of stem stripped off and carried up on the lower margin of the pileus as an imperfect veil. The glebas of all three plants have the foul odor of decaying fish which still persists in the dried specimens after 12 years in the herbarium. The exoperidium was apparently viscid during elongation, since particles of dirt are still firmly attached to portions of its surface.

The area where these plants were collected has been scouted every year since then, but no others have been found.

The California collections. The California area was discovered by the junior author in December 1937 while rabbit hunting but no specimens were taken. In June 1938 both authors visited the area and gathered material, later other trips were made until five collections of *Dictyocephalos attenuatus*, comprising 1129 plants, were obtained. All were growing in a friable soil, ashy in color and texture, on or adjacent to, slightly elevated areas which appear as islands or ridges of land, underlaid by an alkaline clay hard pan. Many plants were in the partial shade of *Atriplex* bushes but the majority were in open naked areas between the *Atriplex* plants.

Four collections were made in and along the sides of a broad shallow wash, over an area of about ten acres; while collection no. 8436, consisting of 80 plants, was found scattered over some 40

acres about ½ mile southwest of the other area in the same type of soil and environment.

Three very unusual specimens were found on the California area; one is a plant with a forked stem (FIG. 12), another is a large thick plant with two small side branches (FIG. 13), while the third specimen has a volva bearing twin plants each perfect in every way.

The California collections have many plants with scales of the exoperidium small and flat, others have flat to erect scales while a few have large erect pyramidal warts (FIG. 2). The outer peridium (not the volva) apparently is fleshy to semigelatinous just before emergence and often very thick on top. As the plant matures and elongates this fleshy layer cracks into scales or warts of varying sizes which are often flattened or otherwise deformed when pushing through the soil, or they may have hardened sufficiently to emerge uninjured. Many exoperidia are horny, reddish and semi-translucent, especially if they were subjected to much pressure when elongating. The degree of this pressure would vary with the hardness of the soil and the depth below the surface at which the plants originated. Exoperidia damaged during emergence usually remain attached to the inner peridium, falling with it when dehiscence occurs.

Many weathered specimens were found, some probably 25 to 30 years old. Only two fungi were observed on these plants, a brownish black mould and a red species of *Gymnoascus*(?) on the old volvas, neither of these fungi caused any evident disintegration of the *Dictyocephalos* tissue. Apparently the main agents in the destruction of the old plants are insects and the action of the elements. Termite work is evident on many and a species of carpenter ant (*Camponotus*) was found in some, but the principal agency in the disintegration of the plants is the weathering action of wind, rain and other climatic factors. The destruction of the plants, however, is a very slow process requiring years before they are finally reduced to soil.

#### GENERAL REMARKS

Data compiled from the various collections show wide variations in this unique species; the three largest plants are 47 cm., 50 cm.

and 56 cm. tall, the three smallest ones 7 cm., 9 cm., and 13 cm., while the usual sizes range from 20-30 cm. in height; 732 stipes are terete, 450 flattened, 241 sulcate; 514 attenuate below, 29 taper upward, 207 are uniform in size throughout, 3 are bulbous at base; 661 are solid while 407 have cavities produced by insects. heads (expanded apices of the stipes) have narrow margins, ranging from 3 to 30 mm. wide, the usual size being 8–10 mm. some plants portions of the margin curve upward for 2-3 cm. like the remnants of a shallow cup (FIGS. 6, 12) but never around the entire rim of the head. The tops of the heads vary as follows, 628 are convex, 47 concave, 91 wedge-shaped, 92 dome-like, 17 flat, and 24 spoon-shaped; in outline, 31 heads are oblong, 32 reniform, 15 arrow-shaped, 7 triangular, the balance are orbicular to oval. Eleven plants have sporocarps split into 2-4 finger-like lobes, each lobe having its own gleba; 1 plant has an annulus (FIG. 3), 2 have veils (Fig. 4), 7 have forked stems (Fig. 12), 6 plants have 1-2 side branches (FIG. 13) while 6 have volvas bearing twin plants.

The scales of the exoperidia vary greatly, ranging from small, thin ones 3–5 mm. across by 0.5 mm. thick (FIGS. 4, 9), as in two of the New Mexico plants, to large pyramidal warts 1–2 cm. broad by 1.5 cm. tall seen in numerous California specimens (FIG. 2) and in the Rhodesian plant. Many have scales intermediate between these two extremes while some have large warts above with small scales around the lower part of the same sporocarp.

The amazing variations in size, shape, scales and other characters of these plants are so many that numerous "new" species could be made from aberrant individuals by writers who believe such characters are valid criteria for differentiating species.

The foetid odor of the gleba so characteristic of this species is present in all the California plants, even in those which had been covered with water for 12 hours during the 1938 floods (March 2–3). Another outstanding character of this species is the tan to white (when weathered) coarsely reticulate-pitted upper surface of the discoid apex or head of the stipe (FIG. 1). This whitish surface consists of a thin (0.1 mm. thick) membrane beneath which is the usual brown color of the stipe context. This thin membrane also lines the entire inside of the endoperidium.

The majority of the plants collected in June 1938 were in open unshaded areas where groups of 2-4 individuals were found emerging from the same hole in the ground which was made by the plants as they elongated; some of the raised blocks of soil weighed 15 pounds. These groups apparently originated from a common underground mycelium, each plant being a complete individual as to volva, stem and sporocarp. The plants of the 1939 crop were not in groups but were solitary and often in more or less shaded places under the edges of the Atriplex bushes.

The California specimens grew in Antelope Valley on the edge of the Mojave Desert—a very hot and arid region—where temperatures during June, July and August range as high as 110 to 115 degrees F. The rainfall for the past ten years has varied from three to twelve inches, the average being near seven inches per year.

#### ACKNOWLEDGMENTS

The writers wish to make grateful acknowledgments to Mr. John A. Stevenson for loan of material, negatives and helpful suggestions on the Bibliography; to Dr. G. D. Darker for aid on the Bibliography; to Mr. and Mrs. Herbert Granquist for aid in collecting specimens; to Floyd R. Schroeder for making the photographs for figures 3, 4, 9, 10; and to W. Carter Maxwell and Glenn R. Haynes of the Division of Grazing for assistance in making the photographs for all the other figures in this article.

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## SEXUALITY IN ACHLYA AMBISEXUALIS

John R. Raper <sup>1</sup> (with 4 figures)

#### INTRODUCTION

Experimental proof of heterothallism in *Dictyuchus*, a genus of the Saprolegniaceae, was given by J. N. Couch (1926) more than twenty years after the discovery of heterothallism in the Mucorales by Blakeslee (1904). Since the publication of Couch's work a similar sexual condition has been demonstrated in two additional genera of the Saprolegniales, *Achlya* and *Sapromyces*. Coker (1927) described *Achlya bisexualis* from the unpublished work of A. B. Couch, and this experimental work was duplicated and confirmed with new isolates by the writer (1936).

Heterothallism was demonstrated in Sapromyces Reinschii by Philip H. Jordan, of Harvard University, during 1927 to 1929. An account of his work has recently been published as a preliminary note by Weston (1938). For a number of years Bishop (1937) has continued and extended the investigation on the sexuality in Sapromyces.

More recently two new "heterothallic" species of Achlya have been described, A. regularis Coker and Leitner (1938) and A. ambisexualis Raper (1939).

Heterothallism in the Mucorales as defined by Blakeslee (1904) and subsequently analyzed by Burgeff (1912) connotes the presence of a single sex in the mycelium and requires the bringing together of two mycelia bearing complementary sexual potentialities before sexual reproduction can be accomplished. In the

<sup>1</sup> Contributions from the Laboratories of Cryptogamic Botany and the Farlow Herbarium, Harvard University, no. 175.

The writer wishes to acknowledge his indebtedness to Professor Wm. H. Weston, Jr., under whose direction the present study was pursued, for his valuable suggestions and criticism.

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germination of the resulting zygote, which has a large number of fusion nuclei, complete segregation of sex takes place insofar as the individual nuclei are concerned, but each spore in the germ sporangium contains several nuclei and hence may have nuclei bearing both plus and minus potentialities. Such a spore, upon germination, gives rise to a thallus of mixed sexual character, known as a heterokaryotic mycelium, with complete segregation taking place in spores subsequently produced.

The sexual condition in the various water molds that have been termed heterothallic does not agree in all respects with conditions first demonstrated in the Mucorales by Blakeslee. An appreciation of the discrepancies existing between allegedly comparable sexual conditions in the two groups necessitates a review of previous work on the water molds.

Couch (1926) found, in *Dictyuchus monosporus*, strains which were  $\mathcal{P}$ ,  $\mathcal{J}$ , parthenogenetic, homothallic, and neuter, all having identical morphological characters. As had been repeatedly noted in the Mucorales, Couch found that the  $\mathcal{J}$  and  $\mathcal{P}$  plants differed widely in their sexual potency. Further, he found that zygotes produced by matings between a  $\mathcal{J}$  and a compatible  $\mathcal{P}$ , gave rise to progeny of four different types. The four types found included (1)  $\mathcal{J}$ , (2)  $\mathcal{P}$ , (3) thalli of mixed sexual potentialities which, however, were predominantly  $\mathcal{J}$  or  $\mathcal{P}$ , and finally (4) sexually inactive mycelia. Oöspores of the parthenogenetic strain gave rise to plants like the parent, which oddly enough, in some few crosses with  $\mathcal{P}$  mycelia, gave a weak  $\mathcal{J}$  reaction with the formation of antheridial branches.

Coker (1927) reported that A. bisexualis has  $\delta$  and  $\mathfrak P$  strains. Raper (1936) showed that in addition to  $\delta$  and  $\mathfrak P$  strains two other strains were involved. Plants were isolated which gave a  $\mathfrak P$  reaction when mated with a compatible  $\delta$ , but which in single spore culture frequently produced abortive oögonia and antheridia. Usually only a few oöspheres were formed in each oögonium and as a rule no oöspores reached maturity. This group of plants was designated hermaphroditic-female. A number of isolates were collected, which were apparently sexually sterile. Since the publication of this account, the author has found two other sexual strains which will be described in detail at a future date.

In Sapromyces Reinschii, the heterothallic condition found by Jordan was again not strictly heterothallism as defined by Blakeslee. Both of and 2 plants were found which reacted sexually when grown together. A number of isolates, however, showed a more complicated sexual condition than a simple bisexual apposition. One isolate produced oögonial initials when grown alone, yet it reacted as a normal  $\mathcal{P}$  when crossed with a plant known to be  $\mathcal{J}$ . Plants which were apparently neuter were isolated by Jordan. Bishop, later working on the same species, found the males to be sexually stable, but certain of the females used in his investigation produced a few oögonia and antheridia in single culture. Fertilization and the maturation of oöspores sometimes occurred. He suggested that these plants were hermaphroditic-females. strains were also found, but it was shown that many of the plants thought to be neuter were capable of giving normal sexual reactions when mated with test plants of strong known sexual characters.

A new species of Achlya, A. regularis, has recently been described as heterothallic by Coker and Leitner (1938). Certain plants of this species, while having definite heterothallic characteristics, at times produced a small number of sexual organs in single culture.

The problem of sexuality in *Achlya* was undertaken by the author at the suggestion of Professors Coker and Couch of the University of North Carolina in 1934, and has been continued since that time in their laboratory and later at Harvard University under the direction of Professor Wm. H. Weston, Jr.

The present paper presents the results of an investigation on the sexuality of A ambisexualis and attempts to interpret and evaluate the sexuality of a number of other water molds previously described as heterothallic.

#### MATERIALS AND METHODS

The material of Achlya ambisexualis used in this investigation comprises the ten isolates from which the description of the species was originally drawn (1939). The isolates were separated on morphological characters into three varieties: type, var. abjointa, and var. gracilis but since varietal differences have not been cor-

related with sexual behavior, designation of the isolates has been based on sexual rather than morphological characters. The origin, collector, date of collection, and variety of each of the isolates are given in Table I.

TABLE I

Isolate	Variety	Place of Collection	Date of Collection	Collector
1 3 2 4	abjointa abjointa gracilis type	Barton Mills, Eng. Chapel Hill, N. C. Blue Hills, Mass. Charles River, Cambridge,	Oct. 1937 Nov. 1935 Oct. 1938 Oct. 1937	R. Emerson J. R. Raper F. T. Wolf S. B. Salvin
5	type	Mass. Charles River, Cambridge, Mass.	Oct. 1937	S. B. Salvin
9	type	Charles River, Cambridge, Mass.	Oct. 1937	S. B. Salvin
10	type	Charles River, Cambridge, Mass.	Oct. 1937	S. B. Salvin
6 7 8	type type type	Oöspore of No. 5 × No. 10 Oöspore of No. 5 × No. 10 Oöspore of No. 5 × No. 10	Apr. 1938 Apr. 1938 Apr. 1938	J. R. Raper J. R. Raper J. R. Raper

The methods used in this study are identical with those previously employed (1936) except for a few modifications. These involved: (1) the use of a known salt solution instead of distilled water treated with animal charcoal, (2) the use of a suitable agar medium for matings in addition to the usual matings in water, and (3) a technique of determining the sexuality of new isolates by a simultaneous mating with known  $\delta$  and  $\Omega$  strains of two species. The importance of these innovations warrants a brief discussion.

Because of the extreme sensitivity of water molds to the dissolved content of the water in which they grow standardization of the medium used in their culture was necessary. A number of water molds, including *Thraustotheca clavata* and several species of *Achlya*, were grown on hemp seed in the various types of water previously employed by other workers. Vigorous growth of the fungi, however, could not be maintained with predictable certainty in any of the various types. Further tests showed that the desired results could be obtained by using Pyrex glass distilled water to which was added a number of inorganic salts in the following concentrations:

		Approximate
Salt	Molarity	Percentage
KH <sub>2</sub> PO <sub>4</sub>	$3 \times 10^{-4}$	0.00045
$MgSO_4$	$1.2 \times 10^{-4}$	0.0003
CaCl <sub>2</sub>	10-5	0.0001
FeCl <sub>3</sub>	$10^{-6}$	0.000016
$ZnSO_4.7H_2O$	10-7	0.000003

The importance of the use of a standardized "water" in experimentation with water molds cannot be over-emphasized, since variations in the kind and amount of dissolved substances present often bring about definite variations in both vegetative and sexual structures.

To verify the results obtained by mating compatible strains in water the same combinations have been made on a favorable nutrient agar medium. Of a large number of media tried, the one found to be the most suitable was the following:

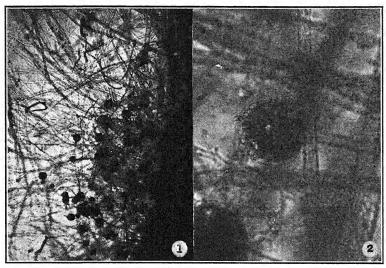
Starch (Soluble)	3 gms.
Peptone (Difco)	1 gm.
Hot water extract of 10 gms. of lentils	
Agar (Difco-Bacto)	20 gms.
Water (containing salts as described above) to	1000 cc.

The use of this agar medium for matings eliminates the most serious objection to matings in water. When the plants are mated in water, zoösporangia are produced in abundance and the liberated zoöspores frequently come to rest on the substrate of the opposed strain and there germinate to form a mycelium which, though small, may produce a few sexual organs. This renders accurate determination of the sexual relationships difficult and can only be obviated by repeating the mating until the same unfortunate event does not occur again. In agar matings only a very few zoösporangia are produced, from which the zoöspores never escape. The region of sexual organs is also better defined and more narrow than in water matings.

Another important advantage of this agar medium is that it greatly facilitates carrying on continued matings free of bacterial contamination.

The sexual potentialities of new isolates were determined in the following manner. Previously determined  $\delta$  and  $\Omega$  strains of both A. bisexualis and A. ambisexualis were inoculated at four equi-

distant locations near the periphery of a plate of lentil agar, with alternating 3's and 2's. Inoculum of the plant to be tested was placed in the center of the plate. After three to four days sufficient growth of all the mycelia had occurred to establish lines of intermingling between the unknown plant in the center and each



Figs. 1, 2. Achlya ambisexualis, sexual strain predominant-female. 1, Portion of mycelium in single pure culture of two weeks. Oʻgʻonia and antheridia produced in small restricted areas, usually in the older parts of the mycelium near the substrate.  $\times$  37. 2, Single oʻgʻonium and attached antheridia. Oʻgʻsphere formation and fertilization occurred as in matings of compatible strains.  $\times$  200.

of the four test plants. One to three additional days were sufficient to indicate the sexual affinities, compatibilities and strength of the previously unknown plant insofar as the reaction in matings with the sexual strains of the two test species could declare those qualities.

Gross water cultures of the isolates were maintained throughout and each was transferred to agar and freed of its contaminants as need for it arose. The technique previously described by the author (1937) was employed to secure bacteria-free mycelia.

#### EXPERIMENTAL STUDIES

From the first observation made on cultures of A. ambisexualis it was apparent that its various isolates and varieties offered exceedingly favorable material for a study of sexuality. Preliminary matings of the isolates showed that strong sexual reactions occurred in certain of the combinations. Apparent heterothallism in the species was thus established early in the work.

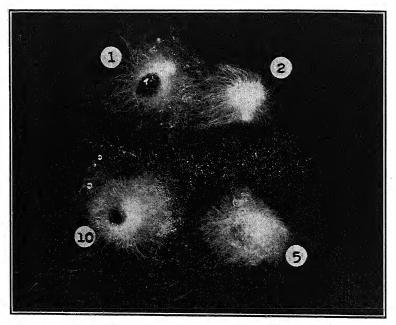


Fig. 3. Water mating of isolates 1 (pure 3), 2 (predominant 3), 5 (predominant  $\Omega$ ), and 10 (pure  $\Omega$ ). Four lines of sexual organs were produced as isolates 2 and 5 each reacted as 3 and  $\Omega$  simultaneously.  $\times$  2.

On fact, however, indicated that the sexual condition was more complicated than a strict separation of  $\delta$  and  $\varphi$  potentialities in two different strains. While four of the 10 isolates remained sexually sterile in single culture, the usual behavior for the sexual strains of heterothallic organisms, the remaining six were weakly and spasmodically self-fertile (hermaphroditic). Single spore cultures of these isolates often produced a small number of oögonial initials in restricted areas 10–15 days after transfer (FIG. 1). In

these areas also developed diclinous antheridial branches. These were attracted to the oʻgonial initials which underwent normal development with the formation of a small percentage of mature oʻgonies (Fig. 2). Those oʻgonial initials not reached by antheridial branches disintegrated. This situation differs in two respects from the production of  $\delta$  and  $\varphi$  organs in a normal homothallic form: (1) here the sexual organs are not produced uniformly over the entire mycelium, and (2) they are not formed when the mycelium is at the height of its vegetative vigor. Although these plants are capable of giving a strong unisexual reaction when mated with certain other isolates, they exhibit only very feeble sexual potency after the hermaphroditic production of sexual organs. The same phenomenon has been described in A. regularis by Coker and Leitner (1938).

Matings of the ten isolates in all possible combinations made clear the inherent bisexual nature of the occasional hermaphroditic isolates. The results of these matings are given in table II.

Beyond indicating the combinations of isolates between which mating will occur the material embodied in table II brings out a number of interesting points that require further explanation. These include: (1) compatibilities, (2) sexual reversals, (3) grouping into sexual strains, and (4) intra-strain sterility and interstrain fertility.

(1). Compatibilities: Each of the ten isolates mated with at least five of the others. Isolates 1 and 2 regularly gave reactions in all of the nine possible combinations for each. Isolates 8, 9, and 10 regularly mated in seven of the nine possible combinations while isolates 3–7 inclusive reacted in five of the possible nine contrasts for each. The fact that two of the isolates mated in all of their possible combinations indicated that at least one of them was reacting as both  $\delta$  and  $\varphi$ .

In all of the matings where a reaction was obtained there was nearly perfect compatibility with well over 90 per cent of the sexual organs produced reaching maturity and with normal oöspores matured in at least an equal percentage.

(2). Sexual reversals: Of the ten isolates used, six, 2–7 inclusive, behaved either as antheridial (3) or oögonial ( $\mathfrak{P}$ ) mycelia depending on the predominant sexual character of the mate. Iso-

TABLE II Isolates

		10	9	8	7	6	5	4	3	2	1		
Isolates	1	III	III	III	III	IV	IV	III	I	I			
	2	IV	IV	IV	III	II	II	I	II		,		
	3	II	III	II		_			*	a.			
	4	IV	IV	III	_		_		•				
	5	IV	IV	II			Leg	end:					
	6	I	III	II		Isolates numbered 1–10 in order of increasing Q and decreasing of							
	7	111	III	ı		potency							
	8			Therefore in each mating isolate with the higher number reacts as $\varphi$									
	9		Mi	Roman numeral indicates relative strength of each reaction  Minus sign indicates no reaction									
	10	(Reactions in vertical columns ♀, in horizontal columns ♂)											

late 2 exhibited strong  $\mathcal{S}$  reactions in eight of its nine combinations while in the ninth, with isolate 1, it reacted as a  $\mathcal{P}$  with the production of functional oögonia. Likewise isolates 3–7 produced oögonia when mated with isolates 1 and 2 and antheridia when contrasted with isolates 8, 9, and 10. The remaining isolates were strictly unisexual, isolate 1 reacted as  $\mathcal{S}$  in all combinations with other isolates and isolates 8, 9, and 10 reacted consistently as  $\mathcal{P}$ .

(3). Grouping into sexual strains: From the data presented above it is possible to place the ten isolates of this species in four sexual strains, the members of each exhibiting identical sexual characters. These strains comprise (a) pure male, isolate 1; (b) predominant male, isolate 2; (c) predominant female, isolates 3–7 inclusive; and (d) pure female, isolates 8, 9, and 10.

(4). Intra-strain sterility and inter-strain fertility: No sexual reaction has ever been observed in matings of isolates belonging to the same sexual strain. All other combinations, however, lead to sexual reactions. Pure male reacts as  $\delta$  to predominant male, predominant female, and pure female, the members of the latter strains reacting as Q in these crosses. Similarly predominant male reacts as  $\delta$  to predominant female and pure female. Finally predominant female reacts as  $\delta$  in matings with members of strain pure female (Fig. 4).

#### SEXUALITY IN AGHLYA AMBISEXUALIS

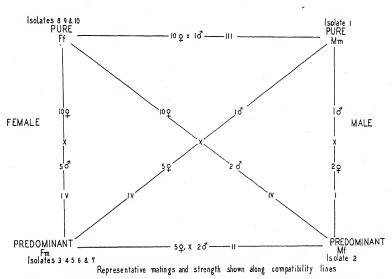


Fig. 4. Diagram of sexual strains in Achlya ambisexualis and the combinations in which matings occur. Along the lines are given representative matings, their relative strength, and the isolate in each reacting as  $\mathcal{S}$  and as  $\mathcal{S}$ .

It is then apparent that all intra-strain combinations are sterile and all inter-strain combinations are fertile. Although the members of both *predominant male* and *predominant female* strains are occasionaly hermaphroditic, the condition here cannot be compared with that found by Ames (1934) in the Ascomycete *Pleurage anserina*. In that species hermaphroditism was regular and constant with compatibility factors governing the ability of two mycelia to react reciprocally.

Further evidence of the bisexual character of isolates belonging to strains predominant of and predominant Q is their behavior in simultaneous inter-strain matings. When isolates 1, 5, and 10 were mated simultaneously in water or on lentil-extract agar, three lines of sexual organs were formed with approximately the same number of oögonia in each line. Isolate 1 reacted as of to both isolates 5 and 10; 10 reacted as 9 to both 1 and 5; thus isolate 5 produced antheridia on the side toward 10 and oögonia in juxtaposition to the mycelium of isolate 1. The same type of simultaneous mating has been made for isolates 1, 2, 5, and 10 both on agar and in water. On semi-solid substrate only three lines of sexual organs have been produced, with isolate 2 reacting only in a & capacity. In water matings, however, four lines of sexual organs have been seen (FIG. 3) with both isolates 2 and 5 behaving simultaneously as  $\delta$  and Q. Thus between the extremes of pure  $\mathcal{S}$  and pure  $\mathcal{S}$  there are at least two intergrades.

#### DISCUSSION

The sexuality of Achlya ambisexualis, like that of other members of the Saprolegniales previously described as heterothallic, differs markedly from that earlier described and defined as heterothallism by Blakeslee (1904). It is entirely possible that a single type of variation from the common heterothallic condition is the rule in this group of plants. In any event sufficient work has been done on these forms to signify that neither the term nor the definition of heterothallism is applicable to the condition encountered.

From the results of previous work and those of the present study it seems that there are six sexual strains with different sexual characters involved in this type of sexuality. These six strains may be expressed as all possible combinations of four sexual factors: F, dominant femaleness; f, latent femaleness; m, latent maleness; and M, dominant maleness. Thus the strains possible could be represented by the following formulae: (1) FM, hermaphroditic and self-fertile with both sexes strong and balanced; (2) Ff, pure female; (3) Fm, predominant-female with male potentialities; (4) Mf, predominant-male with female potentialities; (5) Mm, pure male, and finally, (6) fm, sexually sterile, both sexes weak and

balanced. This grouping of the sexual strains was suggested by Bishop in his doctorate thesis (1937) on sexuality in Sapromyces Reinschii, in which species he found three of these strains, Fm, Mm, and mf.

These formulae as applied here express the sexual characters of the plants of the various strains. No implications of genetic combinations or constitution are intended.

Two of these six strains, Ff, and Mm, are comparable to the ♂ and ♀ strains encountered in strict heterothallic forms. These are constantly sexually sterile in single culture; male and female reproductive organs are formed by them only when they are brought together. The two strains in which one or the other sex is predominant, Fm and Mf, differ from the former by (1) the spontaneous production in single culture of a relatively small number of male and female sexual organs which in most of the cases reported, fail to develop to maturity and (2) the ability of these strains, when crossed with pure of, pure of, or the opposed predominantly sexed plant, to give a reaction opposite that of the predominant sexual potency of the mate. For instance, it has been shown above that strain Fm, isolate 5, of A. ambisexualis will react as a Q to both Mm, isolate 1 pure male, and Mf, isolate 2, predominant-male but will react as a  $\delta$  to strain Ff, isolate 10, pure female. Figure 4 schematically represents these sexual strains and their inter-reactions in A. ambisexualis.

The hermaphroditic self fertile strain, FM, corresponds in its behavior to the forms ordinarily termed homothallic in this and other groups. Finally, the sterile strain, fm, is devoid of sexual expression and reproduces only by asexual and vegetative means. Neither the homothallic nor the sexually sterile strain is represented among the isolates of A. ambisexualis.

The differences between heterothallism, as defined by Blakeslee (1904), and the sexuality in A. ambisexualis, as well as in A. bisexualis, Dictyuchus monosporus, and Sapromyces Reinschii necessitates the introduction of a term more exactly descriptive of the sexual condition of these water molds. To fill this need the writer in connection with the description of A. ambisexualis (1939) suggested the terms gynandromixis or gynandromictic sexuality, implying the mixed sexual character of the various strains

and the capacity of certain of these strains to react as  $\delta^{A}$  or  $\mathcal{P}$  or both.

In the following table a listing of the occurrence of these various strains in the three gynandromictic species which have previously been thoroughly investigated is given in addition to those first described here for *A. ambisexualis*:

TABLE III

SpeciesInvestigator	Dictyuchus monosporus Couch	Sapromyces Reinschii Bishop	Achlya bisexualis Raper	A chlya ambisexualis
FM $Mm$	X		$\times^3$	
Mf	×2	×	$\times^3$	×
Fm Ff	$\overset{\times^2}{\times}$	×	X	×
fm	×	×	×	

 $<sup>^2</sup>$  Certain of Couch's isolates, made from germinated eggs, gave a  $\sigma$  or a  $\varphi$  reaction when mated with strong  $\varphi$  or  $\sigma$  respectively, but each was apparently either predominantly  $\sigma$  or predominantly  $\varphi$ . Although these plants were not observed to produce antheridia and oögonia in single culture, it seems that their inclusion in these groups is entirely logical.

In addition to the six strains listed above, Couch found one which was characteristically parthenogenetic but capable of producing antheridial hyphae when crossed with a strong Q plant, although it showed no reaction when mated with a strong Q.

A similar condition is indicated in at least two species of the Peronosporales. Leonian (1931) showed that homothallic,  $\beta$ ,  $\beta$ , and neuter strains were involved in *Phytophthora omnivora*. He suggested that some or all of the strains probably contained potentialities for both sexes; his results, however, clearly indicate bisexuality only in the homothallic strain. Bruyn (1935, 1937) demonstrated a comparable condition in the obligate parasite *Peronospora parasitica*. In that species were found strains which were homothallic, unisexual (two of these,  $\beta$  and  $\beta$  unidentified because of the growth habit of the fungus), and one which was predominantly of one sex, yet capable of occasional sexual reversals and self-fertility. It does not seem unlikely that the same type of sexuality is common to both the Saprolegniales and the Peronosporales.

<sup>3</sup> Descriptions of these strains as yet unpublished.

Relative sexuality has been shown in the work on A. ambisexualis perhaps as strikingly as anywhere in the fungi, for of ten isolates of that species, six are capable of reacting as either  $\delta$  or  $\mathfrak{P}$ .

Can such reversals and the entire sexual condition be elucidated by the scheme of Hartmann (1925-31) explaining the bisexuality of gametes and the phenomenon of relative sexuality? The theory of relative sexuality as promulgated by Hartmann holds that the gametes (and indeed all other cells of the organism) contain an inherent factor for each sex and that gametes are capable of sex reversibilities depending on the internal and external environmental conditions. His explanation for these phenomena in haplonts such as Ectocarpus and a majority of the Thallophytes postulates the presence of both sex potentialities,  $\beta$  and Q, of equal strength in the zygote or sporophytic generation. In meiosis at the initiation of the gametophytic generation one of these sex potentialities is developed at the expense of the other without, however, rendering it incapable of expression. Such a condition existing in gametes would allow them to behave as unisexual under normal circumstances but when mated with stronger gametes of the same sex would allow their copulation in the opposite capacity. This ability for sex reversibility has been demonstrated in a large number of algae and a few fungi.

This scheme of Hartmann's was originally postulated to apply to those organisms in which ultimate sex determination is dependent on the environmental conditions in the broadest sense. Such sex determination is known as haplophenotypic. Later, however, this concept has been extended to those plants in which final sex determination occurs at the time of meiosis. These are termed haplogenotypic types. Dictyuchus belongs to the latter group according to Kniep (1928) and Hartmann (1931). Since the sexuality found in the other water molds that are not strictly hermaphroditic and self fertile (homothallic in the classical sense) is essentially like that found in Dictyuchus, it may safely be assumed that sexual differentiation in such forms is also genotypically determined. Of course in such forms the worker is not concerned with sexual reversability in the gametes themselves but in the entire mycelia. That is to say, in addition to primary sex characters (behavior of gametes in copulation) as shown in Ectocarpus, the water molds show marked and characteristic secondary sex characters and it is mainly these with which investigators in the aquatic Phycomycetes must deal.

Since the production of gametes is not immediately preceded by meiotic divisions, the mycelium necessarily has nuclei with the same potentialities and components as the gametes. The possibility of the presence of nuclei of different components in the mycelium is strongly opposed by the stability of the sexual characters of the plants over a long period of time and through a number of single-spore generations.

If only the predominantly sexed plants had been found there would be complete agreement between the situation found here and that postulated by Hartmann, but when the entire complex involved is considered there are discrepancies which are significant. Isolates belonging to the Q strains, Ff and Fm, show quantitative differences of the female valence as would be expected from his hypothesis, and that some of the plants are capable of sexual relativity. But in addition to these rather gradual variations of sexual potency or valence, there are constant qualitative differences. These qualitative differences are the points on which the two strains are separated, namely, the ability of the latter to produce sexual organs in single culture and their behavior in inter-strain matings. If there were gradual transitional stages between the two strains, they could be explained on the relative strength of the latent potency, or at least the varying balance between the predominant and the latent potentialities. No such transitional stages have been recorded in any of the gynandromictic water molds. In addition to the two strains which obviously have both of and Q potentialities, Fm and Mf, the work done on this group to date indicates that there are two pure unisexual strains, Ff, and Mm, in which there are apparently no factors allowing for sexual reversibility. In all of the forms studied such pure strains have constantly given only a single reaction in spite of having been mated in all possible combinations with other strains. The possibility that these socalled pure strains have the potentialities of both maleness and femaleness, one very powerful and the other exceedingly impotent in each, must not be overlooked; the points here considered as extremes may be relative rather than absolute. But if this were the case, why are these alleged pure  $\mathcal{J}$  and pure  $\mathcal{L}$  strains so constantly sterile in single culture while only those that have been shown capable of both sexual reactions produce sexual organs of both sexes spontaneously? And why the sharp line of demarcation between them?

Consideration of these points and the additional evidence furnished by the hermaphroditic self-fertile (FM) and the sterile (fm) strains shows that the complex sexuality of these water molds cannot be explained simply on the basis of Hartmann's theory of relative sexuality. The sexuality of these forms, so far as the facts are now known, can be adequately explained by a modified scheme similar to that suggested by Hartmann (1929) and Vandendries (1930) for tetrapolar Hymenomycetes. Complete understanding of the process through which the different strains arise and are perpetuated in nature, however, will depend on further studies on oöspore germination. Although oöspores of Dictyuchus monosporus Couch (1926) and Achlya ambisexualis have been germinated and the progeny tested for sexuality, the limited data from these two cases only serve to emphasize the complex nature of the sexuality in these forms. A genetic study of the progeny of crosses between the strains of A. ambisexualis (six different contrasts) is being carried on by the writer.

#### SUMMARY

A study of sexuality in A. ambisexualis shows that four sexual strains are represented among the isolates of that species: (1) pure  $\mathcal{S}$ , (2) predominant  $\mathcal{S}$ , (3) predominant  $\mathcal{S}$ , and (4) pure  $\mathcal{S}$ . These strains are cross-fertile in all combinations. Plants of the two predominantly sexual strains are weakly self-fertile, and give either a  $\mathcal{S}$  or a  $\mathcal{S}$  reaction when mated, depending on the stronger sexual affinity of the mate. Plants of both predominant  $\mathcal{S}$  and  $\mathcal{S}$  strains have been shown capable of reacting simultaneously as  $\mathcal{S}$  and  $\mathcal{S}$  in different portions of their thalli. In this species sexual reversals are shown as strikingly as anywhere in the fungi.

The six sexual strains found in the various so-called heterothallic species may be expressed as all possible combinations of four sexual factors: M, dominant maleness; m, latent maleness;

f, latent femaleness; and F, dominant femaleness. The combinations possible are: Mm, pure  $\mathcal{F}$ ; Mf, predominant  $\mathcal{F}$ , but also capable of reacting as  $\mathcal{F}$ ; Fm, predominant  $\mathcal{F}$ , capable of reacting as  $\mathcal{F}$ ; Ff, pure  $\mathcal{F}$ ; FM, homothallic, both sexes strong and balanced; and fm, sexually sterile, both sexes weak and balanced.

To differentiate this sexual situation from heterothallism as defined by Blakeslee, the term *gynandromixis* or *gynandromictic* sexuality has been suggested, implying the mixed sexual characters of the thalli of the various strains and the capacity of two of these strains to behave as  $\delta$  and/or Q.

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# SOME NEW SPECIES OF ASCOMYCETES ON CONIFEROUS HOSTS

EDITH K. CASH AND ROSS W. DAVIDSON

(WITH 2 FIGURES)

The fungi here described include one pyrenomycete and four discomycetes collected on conifers in various localities of the United States. Specimens cited are deposited in the Mycological Collections of the Bureau of Plant Industry; type material of the Cenangium has also been sent to the herbaria of the New York Botanical Garden and the University of Michigan and to the Farlow Herbarium of Harvard University.

## 1. Acanthonitschkea coloradensis sp. nov. (FIG. 1, E, F)

Perithecia emerging from the bark in closely packed clusters of 10–50 from a common stroma 1–2 mm. diam., carbonaceous, subglobose to turbinate or pyriform, or contorted by mutual pressure, then collapsing and disciform, black, dull or shining, setose, 200–300  $\mu$  diam., wall 25–50  $\mu$  thick, with circular ostiole 12–15  $\mu$  in diam.; asci cylindrical, apex narrowed and truncate, 70–75  $\times$  4–5  $\mu$ ; spores hyaline, one-celled, 2-guttulate to pseudoseptate, broadellipsoid, obliquely uniseriate, 6–8  $\times$  3–4  $\mu$ ; paraphyses not seen; setae numerous, dark-brown, rigid, short and thick, 15–40 (55)  $\mu$  long, 7–9  $\mu$  thick at the base; stromatic tissue of loosely interwoven, brown hyphae 2–3  $\mu$  thick, becoming more dense and darker at the base of the perithecia; perithecial walls of several layers of thinwalled, brown pseudoparenchyma, dense and black toward the cortex, subhyaline toward the perithecial cavity.

Peritheciis 10–50 in stromate singulo, 1–2 mm. diam. emergenti conglobatis, carbonaceis, subglobosis vel turbinatis, atris, setosis, 200–300  $\mu$  diam., circulariter ostiolatis; ascis cylindricis, apice angustato et truncato, 70–75  $\times$  4–5  $\mu$ ; ascosporis hyalinis, unicellularibus, pseudoseptatis, late ellipsoideis, 6–8  $\times$  3–4  $\mu$ ; setis numerosis, atrobrunneis, rigidis, 15–40 (55)  $\times$  7–9  $\mu$ .

On dead twig of *Abies lasiocarpa* (Hooker) Nuttall, Mesa Lakes, Grand Mesa, Colo., June 1, 1938, R. W. Davidson, F. P. 71992.

<sup>1&</sup>quot;F.P." numbers are those of the Division of Forest Pathology; "Myc. Coll.," the Mycological Collections of the Bureau of Plant Industry.

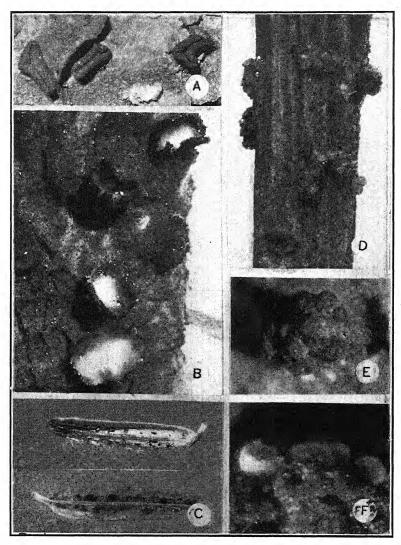


Fig. 1. A, B, Cenangium atropurpureum on Pinus nigra,  $\times$  7; C, Phacidium Tsugae on Tsuga canadensis,  $\times$  5; D, Mollisia Scoleconectriae on Scoleconectria scolecospora on Pinus Strobus,  $\times$  8; E, F, Acanthonitschkea coloradensis and Dasyscypha Acanthonitschkeae on Abies lasiocarpa,  $E \times 20$ ;  $F \times 50$ . (Photographic negatives by M. L. F. Foubert.)

The conidial stage in culture from single ascospores is of the *Cephalosporium* type; cultures after 3 months development on 2.5 per cent malt agar at 11° C. strawberry-pink; hyphae hyaline; conidiophores  $12-35 \times 3-5 \mu$ ; conidia hyaline (pink in mass),  $2-5 \times 1-1.6 \mu$ .

In general structure this fungus seems most closely related to Nitschkia Otth. from which it differs in the spiny perithecia. Of the three genera in the Nitschkeae having setose perithecia. Fracchiaea Sacc. (7) has polysporous asci, and Fitzpatrickia Ciferri (1, p. 29) brown spores; the Colorado fungus is therefore referred to Acanthonitschkea Speg., with which it agrees in the turbinate, collapsing, setose perithecia, the eight-spored asci and the hyaline spores. Both of the two species previously described in this genus are American, A. argentinensis Speg. occurring in Puerto Rico and Argentina, and A. macrobarbata Fitzpatrick in the West Indies (6, p. 62-64). The Colorado species may be distinguished by shorter spines, longer asci, and more sharply delimited stromata with fewer perithecia present on each stroma. The spores of A. coloradensis resemble those of A. macrobarbata in form, rather than the allantoid spores of A. argentinensis. Iridescent mycelium noted as a character of the other two species was not observed in A. coloradensis, although old perithecia from which setae have been rubbed off occasionally show traces of iridescence.

# 2. Dasyscypha Acanthonitschkeae sp. nov. (FIG. 1, E, F)

Apothecia scattered, 1–8 on a single stroma of *Acanthonitschkea coloradensis*, sessile, nearly globose at first, then cup-shaped to subglobose, with circular opening, fleshy-waxy, white, 0.1–0.2 mm. in diameter and height, margin and exterior white-tomentose, hymenium translucent-white; asci cylindrical, rounded at the apex, 8-spored,  $22-24 \times 3-3.5 \,\mu$ ; spores uniseriate, hyaline, one-celled, ellipsoid,  $3.5-4 \times 1.5-2 \,\mu$ ; paraphyses filiform, hyaline, unbranched, not enlarged at the tips; exciple hyaline, prosenchymatous; hairs hyaline, septate, not swollen at the apex, thickly incrusted and verrucose,  $65-90 \times 3-4 \,\mu$ .

Apotheciis sessilibus, globosis dein cupulatis, carneo-ceraceis, albis, 0.1–0.2 mm. diam. et altis, margine et extus albo-tomentosis, hymenio aquoso-albo;

<sup>&</sup>lt;sup>2</sup> Color nomenclature throughout is that of Ridgway, R., Color standards and color nomenclature. Washington, 1912.

ascis cylindricis, apice rotundatis, octosporis,  $22-24\times3-3.5\,\mu$ ; sporis uniseriatis, hyalinis, unicellularibus, ellipsoideis,  $3.5-4\times1.5-2\,\mu$ ; paraphysibus filiformibus, hyalinis; pilis hyalinis, septatis, incrustatis,  $65-90\times3-4\,\mu$ .

On stromata of Acanthonitschkea coloradensis Cash & Davidson on Abies lasiocarpa (Hooker) Nuttall, Mesa Lakes, Grand Mesa, Colorado, June 1, 1938, R. W. Davidsion, F. P. 71992-a.

The only Dasyscypha species described as occurring on pyrenomycetes is D. episphaeria (Mart.) Rehm, in which the dimensions of asci and spores are not recorded; however, it differs from the Colorado fungus in the color of the hymenium. Other species of Dasyscypha with small asci and spores which are reported on coniferous hosts differ also in color and in the presence of a stipe.

## 3. Phacidium Tsugae sp. nov. (FIG. 1, C; 2)

Apothecia hypophyllous, subepidermal, then exposed by the circumscissile removal of the epidermis and widely expanded, broadelliptical to orbicular in outline, honey yellow to isabella color when moist, drying nearly black, 150–275  $\mu$  in diam., 100  $\mu$  in depth; asci

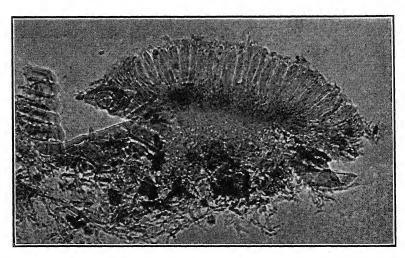


Fig. 2. Phacidium Tsugae, section of apothecium, × about 300. (Photographic negatives by M. L. F. Foubert.)

broad-clavate or subfusoid, narrowing abruptly to a short stipe, broadly rounded at the apex, 8-spored,  $50-65 \times 15-18 \,\mu$ ; spores irregularly and obliquely crowded, one-celled, hyaline, ellipsoid with

obtuse ends, straight or slightly curved, granulose,  $18-22 \times 5-7~\mu$ ; paraphyses filiform, branched and recurved at the tips, with a yellowish mucilaginous coating which joins the tips in a mazaedium; hypothecium 50–60  $\mu$  thick, composed of a dense, pale brownish layer 20  $\mu$  thick immediately below the ascus layer, and an underlying and more loosely interwoven layer 30–40  $\mu$  deep extending into the leaf tissue.

Apotheciis hypophyllis, subepidermicis, epidermide orbiculatim scindenti et hymenium flavidum patefacienti, dein expansis et disciformibus,  $150-275~\mu$  diam.,  $100~\mu$  altis, siccis nigris; ascis late-clavatis vel subfusoideis, abrupte in stipitem brevem attenuatis, apice rotundatis, octosporis,  $50-65 \times 15-18~\mu$ ; ascosporis irregulariter et obliquiter confertis, unicellularibus, hyalinis, ellipsoideo-oblongis, granulosis,  $18-22 \times 5-7~\mu$ ; paraphysibus filiformibus, apice ramosis et recurvatis, in mazaedium flavidulum conglutinatis; hypothecio subhyalino,  $50-60~\mu$  crasso.

On discolored needles of *Tsuga canadensis* (L.) Can., Pineola, N. Car., E. R. Toole, June 24, 1938, F. P. 72022, associated with *Keithia Tsugae* (Farl.) Durand.

A few brownish, pseudo-septate spores, similar to the ascospores in shape and size, were observed embedded in the mazaedium, but none were found in the asci. Their connection with the fungus is doubtful, and, since the spores found in the asci are simple and hyaline, it is described as a species of *Phacidium*. Dearness (3, p. 237) reports occasional septate spores in *P. infestans* Karst.

Tsuga is listed by Faull (4, p. 32; 5, p. 139) among the various genera of conifers attacked by the snow cover Phacidium blight caused by P. infestans. P. Tsugae resembles this species and its variety, P. infestans var. Abietis (3, p. 237), in the dimensions of the asci and spores, but is distinctly different in the manner of opening and the scattered occurrence on the needles as contrasted with the linear arrangement of P. infestans. The widely expanded apothecia are similar to those in P. expansum Davis on Picea Mariana (2, p. 424, pl. 32) and the circumscissile splitting of the epidermis is like that of P. Balsameae Davis (1.c.) on Abies balsamea; both of these species, however, have shorter spores. The opening by a circular lid is a character of the genus Stegopezizella Sydow (9, p. 293–394), based on Phacidium Balsameae; however, a surrounding wall of parallel, black hyphae such as that described for P. Balsameae is lacking in the species on hemlock. Differences

from these and other species of *Phacidium* on conifer needles indicate that the fungus has hitherto not been described.

## 4. Mollisia Scoleconectriae sp. nov. (FIG. 1, D)

Apothecia caespitose on and sometimes completely covering stromata and perithecia of *Scoleconectria scolecospora*, 0.2–0.4 mm. in diam., fuscous black, sessile, soft fleshy, globose with small circular opening, then cupulate, hymenium dark olive gray, margin fimbriate, incurved when dry; asci cylindrical-clavate, with apex broadly rounded, 8-spored,  $25-35\times3-4~\mu$ ; spores biseriate, hyaline, unicellular, narrow-cylindrical, straight or slightly curved,  $5-7\times1~\mu$ ; paraphyses filiform, hyaline, unbranched,  $1~\mu$  in diameter; hypothecium hyaline, prosenchymatic, about  $25~\mu$  thick; exciple brown, pseudoparenchymatic at the base, gradually changing into free, hyaline hyphae at the fimbriate margin.

Apotheciis in stromatibus et peritheciis *Scoleconectriae scolecosporae* dense caespitosis, 0.2–0.4 mm. diam., atro-brunneis, nigrescentibus, sessilibus, globosis, cupulatis, hymenio cinereo, margine fimbriato; ascis cylindricis, apice late rotundatis, octosporis,  $25-35\times 3-4\mu$ ; sporis biseriatis, anguste cylindricis, hyalinis, continuis, rectis vel leniter curvatis,  $5-7\times 1\mu$ ; paraphysibus filiformibus, hyalinis, non ramosis,  $1\mu$  diam.; contextu excipuli basi pseudoparenchymatico, marginem versus hyphas elongatas, hyalinas exeunte.

On stromata of *Scoleconectria scolecospora* (Bref.) Seaver on twigs of *Pinus Strobus* L. near Stone Creek, Huntingdon Co., Pa., Feb. 19, 1933, L. O. Overholts and R. W. Davidson, F. P. 86440 (type), near State College, Pa., L. O. O. and R. W. D., Apr. 27, 1940, F. P. 86479, and Norwich, N. Y., Apr. 25, 1933, R. W. D., F. P. 86445.

Macroscopic examination of herbarium specimens of *Scoleconectria* has failed to show the presence of this *Mollisia*; however, it may easily have been overlooked, since the small and inconspicuous apothecia might readily be mistaken for old darkened perithecia of the host fungus. This species is distinct from all of the dozen or more species of *Mollisia* found on *Pinus*, both in its occurrence on *Scoleconectria* and in its morphology, particularly in its narrow spores.

## 5. Cenangium atropurpureum sp. nov. (FIG. 1, A-B)

Apothecia 2–5 mm. in diam. and height, erumpent singly or two or three together from stroma beneath the bark, subglobose then cupulate, fleshy-leathery, substipitate, exterior furfuraceous, dull purplish black to fuscous black when moist, raisin black when dry; margin lacerate, becoming inrolled when dry and apothecia triangular or hysteroid; hymenium light ochraceous buff to chamois colored; asci cylindrical, apex flattened with pore usually toward one side, 8-spored, 70–85  $\times$  9–12  $\mu$ ; spores broad-ellipsoid, irregularly uniseriate, hyaline, one-celled, containing several small scattered guttules, 9.5–11  $\times$  5–8  $\mu$ ; paraphyses hyaline, unbranched, enlarged at the apex to 3–5  $\mu$ ; hypothecium 20–30  $\mu$  thick, prosenchymatic, pale brownish; intermediate layer plectenchymatic, 100–150  $\mu$  thick, of hyaline, thick hyphae; cortex 100–200  $\mu$  thick, black, dense, furrowed and lacerate on the surface.

Apotheciis 2–5 mm. diam. et altis, erumpentibus, subglobosis dein cupulatis, carneo-coriaceis, furfuraceis, atropurpureis, margine lacerato, hymenio ochraceo; ascis cylindricis, octosporis,  $70-85\times9-12\,\mu$ ; sporis late ellipsoideis, hyalinis, unicellularibus, guttulatis,  $9.5-11\times5-8\,\mu$ ; paraphysibus hyalinis, simplicibus, apice usque  $3-5\,\mu$  inflatis; hypothecio pallide brunneolo; cortice atro, lacerato.

On dead twigs of *Pinus nigra* Arnold, Sugar Loaf Mt., Md., Apr. 25, 1935, R. W. Davidson and M. E. Fowler, F. Path. 59167 (type); P. Mugo Turra, P. pungens Lambert, P. rigida Miller, and P. virginiana Miller, Maryland; P. taeda L., Georgia; P. sylvestris L., Pennsylvania, in Herb. L. O. Overholts 15611.

In the dimensions of the asci and spores this *Cenangium* is close to *C. Abietis* (Pers.) Rehm, common on various coniferous hosts. The apothecia, however, are larger than is usual in the latter species, which Schwarz (8, p. 47) reports as 1.5–2.5, rarely 3 mm., in diameter. The purplish color is a feature not noted for *C. Abietis* or other species of *Cenangium* described on conifers.

No conidia have been observed on the twigs or in pure cultures grown on 2.5 per cent malt agar. The mycelium in culture is not as dark as is the mycelium of *C. Abietis* from *Pinus ponderosa* Lawson, which on the same medium produced an abundance of conidia.

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# SOME DERMATEA SPECIES AND THEIR CONIDIAL STAGES 1

J. Walton Groves 2

(WITH 13 FIGURES)

The genus *Dermatea* is characterized principally by the dark colored, leathery apothecia occurring on twigs and branches of woody plants, ellipsoid to ellipsoid-fusiform ascospores, and the presence of a definite epithecium. The conidial stages of *Dermatea* species are usually referred to the form genus *Micropera*, which typically consists of a waxy-fleshy stroma containing one to several cavities bearing elongate-fusiform to sub-filiform conidia. Tulasne (1865) first drew attention to the association of *Micropera* species with *Dermatea* species, and observed the two stages arising from the same basal stroma. This association has also been noted by von Höhnel (1916), Nannfeldt (1932), Seaver and Velasquez (1933), and others. The genetic connection has been generally accepted, although definite proof based on cultural studies has been lacking for the most part.

The species described in this paper were collected chiefly in the Temagami Forest Reserve, Ontario, and in the vicinity of Toronto, Ontario. Cultures were obtained from both ascospores and conidia and were grown on two per cent malt extract agar and on sterilized twigs of the host. The cultures from ascospores and conidia were similar in appearance and both produced the same conidial stage in culture. This was considered proof of genetic connection.

Dermatea Molliuscula (Schw.) Cash, Mycologia 29:304. 1937. Cenangium molliusculum Schw. Trans. Am. Phil. Soc. II. 4: 239. 1832.

<sup>&</sup>lt;sup>1</sup> Contribution No. 615 from the Division of Botany and Plant Pathology, Science Service, Department of Agriculture, Ottawa, Canada. Part of the work was done at the Department of Botany, University of Toronto, and was included in a thesis presented to the School of Graduate Studies of that University in partial fulfilment of the requirements for the degree of Doctor of Philosophy.

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Gelatinosporium fulvum Peck, Ann. Rep. N. Y. State Mus. 38: 97. 1885.

A description of this species based partly on the writer's material was recently published by Miss Cash (1937) and it seems unnecessary to re-describe it now. It occurs on *Betula* species,

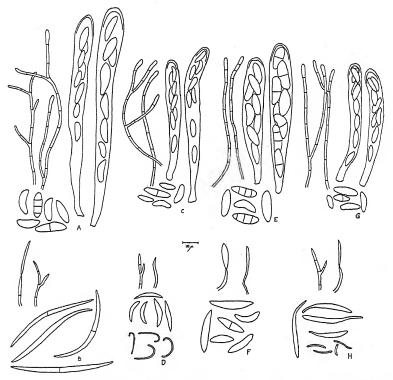


Fig. 1. A, B, Dermatea molliuscula; C, D, D. Ariae; E, F, D. Hamamelidis; G, H, D. Viburni.

apparently most commonly on *B. lutea* Michx. The specimens examined in this study are listed below.

Specimens examined: University of Toronto Herbarium. On *Betula lutea*. 3525 (46), 8430 (193), Temagami Forest Reserve, Ontario—6773 (278), south of Aurora, Ontario.

 $<sup>^{\</sup>rm 3}$  The numbers in parentheses refer to duplicate specimens in the herbarium of J. W. Groves.

Mycological Herbarium, Science Service, Department of Agriculture, Ottawa, Ont. On *Betula lutea*. 3917, Chelsea, Que.—3918, Burnet, Que.—4694 (552), North Halton, Nova Scotia—5317 (599), Duchesnay, Que. On *B. papyrifera*. 2595 (440), Chelsea, Que.

Herbarium of J. W. Groves. On *Betula lutea*. 186, Temagami Forest Reserve, Ont. On *Betula* sp. 514, Colch. Co., Nova Scotia, ex herb. L. E. Wehmeyer 1287a—532, Holl Pond, N. Y., ex herb. Univ. of Michigan, Coll. C. H. Kauffman and E. B. Mains, Aug. 24, 1914—656, Lycoming Co., Penn., ex herb. L. O. Overholts 21611.

Ex Herbarium N. Y. Bot. Garden, unnumbered, Randolph, N. H. June 22, 1927 (as *Dermatea Betulae* Rehm).

Durand Herbarium. 3933, ex herb. Schweinitz, marked part of type.

On malt extract agar the colonies reach a diameter of 3–3.5 cm. in four weeks. They are whitish at first, then variously colored and more or less zoned with shades of olive, yellow, green, or brown, darker in the centre, the aerial mycelium short, even, and velvety. The conidial stromata are usually almost globose, up to 5 mm. in diameter, downy to velvety, whitish, buff, or yellowish, usually containing several lobed cavities which tear open irregularly. The tissue is composed of closely interwoven, hyaline hyphae about 2.5–4.0  $\mu$  in diameter, looser at the outside. The conidiophores are hyaline, cylindric, septate, branched, 1.5–2.0  $\mu$  in diameter, mostly 15–30  $\mu$  in length, sometimes longer, tapering to a fine point. The conidia are hyaline to pale yellowish, sub-filiform, sickle-shaped or sigmoid to almost straight, ends pointed, one to four celled,  $50–75 \times 2.5–3.5 \mu$ . No microconidia have been observed.

On twigs of *Betula* very little aerial mycelium is produced, sometimes a few whitish to buff or grayish-brown tufts appear at the point of inoculation. The conidial stromata are strongly erumpent, rounded, sub-globose or slightly elongated, up to 4 mm. in diameter and 2 mm. in height, whitish to buff, yellowish, olivaceous, or brownish, covered with a short, downy mycelium. The structure is very similar to fruiting bodies of *Gelatinosporium fulvum* as found in nature.

This species is characterized chiefly by its occurrence on *Betula*, the strongly erumpent, often laterally fused apothecia, the long asci, and the type of conidial stage. It was first described by Schweinitz (1832) as *Cenangium molliusculum*, and transferred to *Dermatea* by Cash (1937).

This fungus was described and figured by Seaver and Velasquez (1933) who erroneously identified it as *Dermatea Betulae* Rehm. Dr. Seaver kindly sent a specimen of their fungus for examination and it is unquestionably *D. molliuscula*. *D. Betulae*, which was described by Rehm (1896), is a *Pezicula* and was subsequently transferred to that genus by Rehm (1912). The type of *D. Betulae* Rehm was collected and distributed by Sydow in Myc. March. 4359, and another specimen also collected by Sydow was distributed in Syd. Myc. Germ. 2165. Both of these specimens have been examined and are a *Pezicula* and quite distinct from *D. molliuscula*.

Seaver and Velasquez (1933) observed the association of their fungus with *Gelatinosporium fulvum* Peck and concluded that it was the conidial stage. Cultural studies have shown this to be correct. There is no valid distinction between *Micropera* and *Gelatinosporium* and this is a typical *Micropera*.

DERMATEA ARIAE (Pers.) Tul. Sel. Fung. Carp. 3: 160. 1865.

Pesisa Ariae Pers. Myc. Eur. 1: 325. 1822.

Tourbania Asias Esias Crest Mars 2. 175 1926

Tympanis Ariae Fries, Syst. Myc. 2: 175. 1822.

Tympanis inconstans Fries, Summa Veg. Scand. 400. 1849.

Cenangium inconstans Fuckel, Symb. Myc. 268. 1869-70,...

Cenangium subnitidum Cooke & Phill. Grevillea 3: 186. 1875. Phacangella subnitida Massee, Brit. Fung. Fl. 4: 137. 1895.

Sphaeria Cotoneastri & Sorbi Fries, Syst. Myc. 2: 494. 1823.

Micropera Sorbi Sacc. Michelia 2: 104. 1880.

Sphaeronema pallidum Peck, Ann. Rep. N. Y. State Mus. 25: 85. 1873.

Apothecia erumpent, gregarious, separate or in small clusters of two to four, circular or undulate, sessile, narrowed below, 0.4–0.8–(1.0) mm. in diameter, 0.2–0.4 mm. in height, dark reddish-brown to black, slightly furfuraceous to glabrous, hard, leathery to horny in consistency, more fleshy-leathery when moist, hymenium concave to plane, black, with a thick, raised, brownish margin; tissue

of the hypothecium compact, pseudoparenchymatous, composed of irregular thick-walled cells, 3–8  $\mu$  in diameter, arranged in more or less vertically parallel rows, curving obliquely toward the outside where the cells are darker and thicker walled, subhymenium a narrow, indefinite zone of slender, interwoven hyphae; asci cylindric-clavate, narrowed into a short stalk, eight spored, (60)–70–90–(100)  $\times$  8–10  $\mu$ ; ascospores ellipsoid-fusiform, hyaline to pale yellowish, one to four celled, straight or slightly curved, irregularly biseriate to uniseriate below, (10)–12–18–(22)  $\times$  3–5  $\mu$ ; paraphyses hyaline, filiform, septate, simple or branched, 1.5–2.5  $\mu$  in diameter, the tips swollen up to 5  $\mu$  and glued together forming a

yellowish epithecium.

Conidial fruiting bodies erumpent, gregarious, usually separate, sometimes two or three together, bluntly conical, about 250–350  $\mu$  in diameter at the base, 250–500  $\mu$  in height, reddish-brown to olivaceous or black, slightly furfuraceous to glabrous, hard, horny in consistency, becoming softer and more fleshy when moist, containing a single, ovoid or slightly chambered cavity; tissue pseudoparenchymatous in the basal stroma, composed of irregular, hyaline cells about 3–6  $\mu$  in diameter, becoming prosenchymatous above, composed of ascending, parallel to more or less interwoven hyphae 2–3  $\mu$  in diameter, brownish at the outside; conidiophores hyaline, cylindric, simple or branched, continuous or septate, pointed at the tip, 20–40  $\times$  1.5–2.0  $\mu$ ; conidia hyaline to pale yellowish-green, elongate-fusiform, sickle-shaped, occasionally sigmoid or almost straight, ends pointed, one or two celled, (12)–15–20–(25)  $\times$  2.0–4.0  $\mu$ , microconidia not observed in nature.

Host: Sorbus spp.

Exsiccati: Krieg. Fung. Sax. 1516; Rehm Ascom. 1057; Roum. Fung. Sel. Gall. Exs. 537; Phill. Elv. Brit. 94 (as Cenangium subnitidum Cooke & Phill.); Syd. Myc. Germ. 1992 (Micropera Cotoneastri (Fries) Sacc.); Fung. Columb. 571.

Specimens examined: University of Toronto Herbarium. On Sorbus americana. 4495 (68), 4496 (69), 7283 (180), 7918 (332), 7921 (406), 7922 (331), Temagami Forest Reserve, Ontario.

Herbarium of J. W. Groves. On Sorbus americana. 235, 296, 628 (ex herb. L. O. Overholts 18873), Temagami Forest Reserve, Ont.—609, 626 (ex herb. U. S. D. A. Path. and Myc. Coll. C. L. Shear 4161), Duchesnay, Que.—641 (L. E. Wehmeyer 402), Truro, Nova Scotia. On Sorbus aucuparia. 577, Uppsala, Sweden, coll. L. E. Wehmeyer, Aug. 18, 1937.

On malt extract agar the colonies reach a diameter of 5-6 cm. in three weeks. The margin is almost colorless and closely appressed. The aerial mycelium is at first thin, whitish, cottonyfluffy, becoming much more abundant toward the centre of the colony, much tufted, and variously colored from whitish to pale yellow, ochraceous, or "clay color" to "olive ocher" (Ridgway). Conidial fruiting bodies are produced only occasionally as fleshy stromata, usually about the size and shape of those found in nature, but sometimes much larger and almost globose. They are whitish to yellowish or buff, covered with a short, downy mycelium, and usually containing a single, more or less lobed cavity, the larger fruiting bodies splitting open very widely. The tissue is composed of closely interwoven hyphae. Occasionally cultures will be obtained which grow more slowly and produce less aerial mycelium, but these produce the same type of conidial fruiting body and spores; in fact they seem to fruit more readily than the commonly obtained colony with more aerial mycelium. The conidia and conidiophores are typical of those found in nature. Microconidia are hyaline, filiform, usually more or less hooked at one end, one celled,  $10-20-(25) \times 1.5-2.0 \mu$ .

On twigs of *Sorbus* some whitish to buff aerial mycelium is developed at the point of inoculation and may spread more or less over the twig. Conidial fruiting bodies arise as small, erumpent, fleshy stromata, at first rounded, tomentose, then becoming more or less flask-shaped to conical, blackish and glabrous above, about 0.5 mm. in diameter at the base, and the same in height. They do not sporulate very freely, most of them remaining sterile and developing into large, cottony, mycelial tufts. The tissue structure is similar to that found in nature, the conidia and conidiophores are typical and microconidia have been observed.

This species is characterized chiefly by its occurrence on *Sorbus*, brownish to black, not strongly erumpent apothecia, small asci and ascospores, the type of conidial fruiting body and the short, slender conidia. It has been known for a long time in Europe where it is apparently more common than in North America. The conidial fruiting bodies are usually more abundant, and frequently more conspicuous than the apothecia. The genetic connection of the two stages has long been assumed, but proof based on cultural

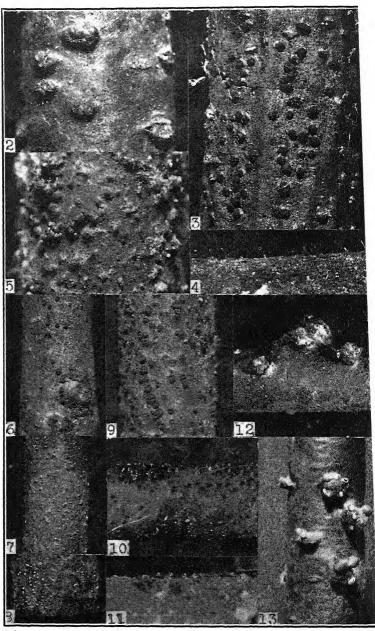


Fig. 2, Dermatea molliuscula; 3–5, D. Viburni; 6–8, D. Hamamelidis; 9–11, D. Ariae; 12, 13, D. molliuscula.

studies has hitherto been lacking. Von Höhnel (1916) has given a list of synonyms of the conidial stage.

Cenangium subnitidum Cooke & Phill., which is here included as a synonym, was originally described by Cooke (1874) from a specimen said to be on Alnus and distributed in Phill. Elv. Brit. 94. Examination of the specimen in the Farlow Herbarium disclosed that it was identical with Dermatea Ariae. Both perfect and imperfect stages were present and agreed with the original description of C. subnitidum. At the writer's request, the wood of the host was examined by Dr. R. H. Wetmore who stated that it was definitely not Alnus but Sorbus. Thus there can be no doubt that C. subnitidum was based on a misdetermination of the host.

### Dermatea Hamamelidis (Peck) comb. nov.

Patellaria Hamamelidis Peck, Ann. Rep. N. Y. State Mus. 33: 32. 1880.

Dermatella Hamamelidis Durand, Bull. Torrey Club 29: 464. 1902.

Dermatella Hamamelidis Ellis & Ev. Proc. Phila. Acad. Sci. 45: 149. 1893.

Lecanidion Hamamelidis Sacc. Syll. Fung. 8: 800. 1889.

Apothecia erumpent, scattered or more or less in rows, separate or in small clusters, circular or somewhat undulate, sessile, narrowed below, 0.3-0.8 mm. in diameter, 0.2-0.4 mm. in height, dark reddish-brown to black, hard, leathery to horny in consistency, becoming more fleshy-leathery when moist, hymenium concave to plane or finally convex, slightly roughened, margin at first raised, later almost disappearing; tissue of the hypothecium compact, pseudoparenchymatous, composed of more or less elongated to almost isodiametric cells  $5-12 \mu$  in diameter, fairly thick walled, dark brown to almost hyaline, arranged in more or less vertically parallel rows, curving obliquely toward the outside where the cells are smaller, darker, and thicker walled; subhymenium a narrow zone of filamentous, interwoven hyphae; asci cylindric-clavate, short stalked, eight spored,  $(70)-80-100-(120) \times (10)-12-15 \mu$ ; ascospores ellipsoid-fusiform, hyaline to yellowish, straight or slightly curved, irregularly biseriate, one to four celled, (13)–15–20–(22)  $\times$  5.0–7.5  $\mu$ ; paraphyses hyaline, filiform, septate, simple or branched, 1.5-2.0 μ in diameter, the tips slightly swollen and glued together forming a vellowish epithecium.

Conidial fruiting bodies minute, about 150-200  $\mu$  in diameter.

developing beneath the outer bark layers and splitting them, appearing as small, thickly scattered, blister-like elevations in the bark with gray spore masses emerging through them when moist. In section they appear as an acervulus-like structure with a thin basal layer about 5–8  $\mu$  in thickness, composed of hyaline, indistinct, slender, interwoven hyphae which curve upwards to form the hyaline, cylindric, simple conidiophores, 10–25  $\times$  2.0  $\mu$ , tapering to a slender tip; conidia elongate-fusiform to sub-filiform, hyaline, one or two celled, straight or curved, sometimes one end narrower and more curved than the other, (15)–18–25–(32)  $\times$  4.5–6.0  $\mu$ . No microconidia have been observed.

Host: Hamamelis virginiana L.

Exsiccati: Ellis N. Am. Fungi 2634; Fung. Columb. 2016.

Specimens examined: University of Toronto Herbarium. On *Hamamelis virginiana*. 4374 (57), 7402 (162), 6565 (271), 7928, Toronto, Ont.—unnumbered (285), Pixley's Falls, N. Y. Coll. R. F. Cain.

Herbarium of J. W. Groves. On *H. virginiana*. 661 (ex herb. L. O. Overholts 21692), Stoyestown, Pa.—667 (ex herb. L. O. Overholts 20139), English Center, Lycoming Co., Pa.

Durand Herbarium. 6096, N. Greenbush, N. Y. Part of the type. 1048, Lyndonville, N. Y. Coll. C. E. Fairman (as Dermatella Hamamelidis Ell. & Ev.).

On malt extract agar the fungus grows very slowly reaching a diameter of 2–2.5 cm. in five weeks, forming heaped up colonies of firm consistency with a more or less wavy margin. The surface is often deeply radially furrowed, sometimes even, very variable in color, whitish to buff, yellowish-green, brown, or almost black. The conidial fruiting bodies are small, almost globose stromata,  $300-400~\mu$  in diameter, composed of closely interwoven, hyaline hyphae about  $3-5~\mu$  in diameter, and containing a more or less lobed cavity. The walls surrounding the cavity are about  $25-50~\mu$  in thickness and they tear open widely at the top. The conidia are typical but the conidiophores are sometimes longer than in nature.

On twigs of *Hamamelis* very little aerial mycelium is produced, but sometimes a little whitish to buff or brown, closely appressed aerial mycelium develops around the point of inoculation. The conidial fruiting bodies are small, erumpent, rounded stromata, whitish to buff, about  $250-400 \mu$  in diameter, covered with a short.

aerial mycelium. The microscopic structure is similar to those formed on agar. No microconidia have been observed.

This species is characterized by its occurrence on *Hamamelis*, small, blackish, not strongly erumpent apothecia, relatively short and broad conidia, and the type of conidial fruiting body. As far as known the conidial stage is undescribed but it may be regarded as a reduced *Micropera*.

This fungus was first described by Peck (1880) as Patellaria Hamamelidis and transferred to Dermatella by Durand (1902). In the meantime Ellis and Everhart (1893) had described it independently as a new species of Dermatella. The genus Dermatella was erected by Karsten (1871) and separated from Dermatea by having septate ascospores. Since it is possible to find septate ascospores in all Dermatea species including D. Cerasi (Pers.) Fries, the type of the genus, this cannot be regarded as a valid generic distinction. Dermatella must, therefore, be regarded as a synonym of Dermatea and it is necessary to transfer this species to Dermatea.

### Dermatea Viburni sp. nov.

Sphaeronema hystricinum Ellis, Bull. Torrey Club 6: 106. 1876. Sphaerographium hystricinum Sacc. Syll. Fung. 3: 597. 1884. Chondropodium hystricinum Höhnel, Frag. Myk. 958. 1916. Sphaerographium hystricinum var. Viburni Dearn. & House, Bull. N. Y. State Mus. 197: 35. 1917.

Apotheciis erumpentibus, sparsis, solitariis vel 2–6 congregatis, sessilibus, versus basim leviter attenuatis, orbicularibus vel undulatis, parvis, 0.3–0.6 mm. diam., 0.2–0.5 mm. altis, atris, duris, coriaceis vel corneis, in humido carnosocoriaceis; hymenio atro, primitus concavo dein plano vel convexo, margine initio elevato dein evanescente; hypothecio prosenchymato; ascis cylindraceoclavatis, breviter stipitatis, octosporis, (50)–60–75 × 8–12.5  $\mu$ ; ascosporis ellipsoideo-fusiformibus, hyalinis vel leviter fuscis, rectis vel leviter curvatis, continuis vel uniseptatis, irregulariter biseriatis vel subuniseriatis, (10)–14–18–(20) × 3.5–5.5  $\mu$ ; paraphysibus hyalinis, filiformibus, septatis, ramosis, 1.5–2.0  $\mu$  diam., apice ad 3  $\mu$  leviter incrassatis, epithecium formantibus.

Apothecia erumpent, separate or in small clusters of 2–6, sessile, slightly narrowed below, circular or slightly undulate, 0.3–0.6–(1.0) mm. in diameter and 0.2–0.5 mm. in height, dark brown to black, hard, leathery to horny in consistency, becoming more fleshyleathery when moist; hymenium black, at first concave, becoming plane to convex, margin at first raised, later almost disappearing;

hypothecium composed of closely interwoven, hyaline to pale brownish, thick-walled hyphae about 5-8 µ in diameter, in the upper part more or less vertically parallel, curving obliquely toward the outside where the walls are darker colored; subhymenium a narrow, brownish zone; asci cylindric-clavate, short stalked, eight spored, (50)-60-75  $\times$  8-12.5  $\mu$ ; ascospores ellipsoid-fusiform. hvaline becoming slightly vellowish, straight or slightly curved, one or two celled, (10)-14-18-(20)  $\times$  3.5-5.5  $\mu$ ; paraphyses hyaline, filiform, septate, much branched,  $1.5-2.0 \mu$  in diameter, the tips slightly swollen up to 3 µ and glued together forming a vellowish

epithecium.

Conidial fruiting bodies erumpent, thickly scattered or more or less in rows, single or with two or three arising from the same basal stroma, cylindric-subulate, dark brown to black, often with a reddish tinge, especially when moist, base about 0.3-0.5 mm, in diameter and the beaks about 1 mm. long, hard, leathery to horny. becoming more fleshy when moist: tissue of the basal stroma composed of closely interwoven, ascending, hyaline, thick-walled hyphae about 5-8  $\mu$  in diameter, becoming darker colored and thicker walled at the outside, tissue of the beak similar in structure, the basal stroma containing a single, ovoid to elongated cavity about 150-250 μ in diameter; conidiophores cylindric, septate, occasionally branched, tapering to a slender point,  $15-30 \times 2.0-2.5 \mu$ , lining the cavity and the beak; conidia elongated to sub-filiform, hyaline, sickle-shaped or sigmoid to almost straight, usually with one end more attenuated than the other, one celled,  $(25)-30-45 \times 2.5-4.0 \mu$ . No microconidia have been observed in nature.

Host: Viburnum species.

Type: University of Toronto Herbarium 7937, Hatchley, Ontario.

Exsiccati: Ellis, N. Am. Fungi 337 (Sphaerographium hystricinum); Rel. Farl. 198a, 198b (S. hystricinum).

Specimens examined: University of Toronto Herbarium. On Viburnum Lentago L. 7937 (433), Hatchley, Ont. On V. cassinoides L. 4460, 4461, 6976 (230), 8432, Temagami Forest Reserve, Ont.-4558, Wilcox Lake, Ont.-7171, 7266 (275), north of Parry Sound, Ont.—unnumbered, 7th Lake, Inlet, N. Y. On V. nudum L. ex Farlow Herbarium, Abbey Rd., Ripton, Vt. Coll. E. A. Burt, Mar. 6, 1897.

Herbarium of J. W. Groves. On V. cassinoides L. 268, Temagami Forest Reserve, Ont.—600, Duchesnay, Oue.

On malt extract agar the cultures grow slowly, reaching a diameter of 2.5-3.0 cm. in three weeks. The colonies are very irregular with a lacerate margin, whitish at first, then brownish or buff to avellaneous. The aerial mycelium is usually short, downy to velvety, sometimes almost absent, occasionally forming whitish, cottony tufts. Conidial fructifications are similar in both ascospore and conidial cultures. In color and consistency they are similar to those found in nature, but they do not develop the characteristic beaks. They are very irregular in shape and unevenly rounded, up to 3 mm. in diameter and 1 mm. in height, glabrous, with one or more irregular openings through which the conidia emerge in gravish-white masses. The tissue of the stroma is composed of hyaline or slightly colored, closely interwoven hyphae about  $3-5 \mu$ in diameter. A striking feature is the presence of a deep red pigment irregularly distributed throughout the stroma but especially in the upper part surrounding the pycnidial cavities. These cavities are irregular in shape and more or less lobed, finally opening very widely. The conidia are typical of those found in nature, the conidiophores sometimes longer. Microconidia hyaline, filiform, mostly curved, one celled,  $8-15 \times 1.5-2.0 \mu$ .

On twigs of Viburnum very little aerial mycelium is produced. Conidial fructifications which exhibit considerable variation in the form of the stroma are developed, and none have been observed quite typical of the form as it occurs in nature. The fruiting bodies are erumpent, rounded or irregular in shape, about 0.5-1.0 mm. in diameter, reddish-brown to black, glabrous or covered with a short, brown, aerial mycelium. Many do not elongate but split open irregularly, while others become more or less elongated, up to 2 mm. in height. They are thicker than in nature and may open at the top or remain sterile. Sometimes a cluster of short beaks will arise from one basal stroma which may be up to 2 mm. in diameter. The stroma frequently continues to develop vegetatively, eventually forming erect, brown, cottony tufts scattered over the twigs and never sporulating. The tissue structure is similar to that found in nature but the hyphae are sometimes thinner walled and more loosely interwoven, especially toward the outside. The cavities are more irregular in shape and frequently more or less lobed. The conidia and conidiophores are typical but the latter may be longer than in nature.

This fungus is common on Viburnum in the Temagami Forest Reserve but usually only the conidial stage is found. The apothecia were only discovered after much search for a perfect stage and are usually very scarce and much less conspicuous than the conidial fruiting bodies. Apothecia of Tympanis fasciculata Schw. are frequently found on the same twigs and are somewhat similar in gross appearance, but can readily be distinguished by the many-spored asci and have a Pleurophomella species as the conidial stage. Dermatea minuta Peck is a Pezicula and has a Cryptosporiopsis species as the conidial stage. Dermatea viburnicola Ellis is an Encoelia, and has only produced a microconidial stage in culture. No fungus described on Viburnum appeared to agree with this species which is accordingly described as new.

Sphaerographium hystricinum was originally described by Ellis (1876) and said to be on Viburnum. The description by Saccardo (1884), however, gives the host as Azalea viscosa. Peck (1885) reported it on Viburnum nudum and his figures unquestionably illustrate the fungus studied here. Dearness and House (1917) apparently following Saccardo and regarding the Azalea form as the type, re-described the Viburnum form as a new variety. It is possible that this, or a similar species, may occur on Azalea, but I have seen no material on this host and cultural studies would be necessary before a final decision as to its identity could be reached. Von Höhnel (1916) suggested that S. hystricinum would prove to be the conidial stage of a Godronia, but the cultural studies have demonstrated that it belongs to a Dermatea.

The four species of *Dermatea* described above were chosen for the purpose of illustrating some of the range of variation in the form of the conidial stroma in this genus. The range of variation in the form of the conidial stroma of species of the related genus *Pezicula* was described by the writer (1939), and it was noted that on the basis of the form of the conidial stroma, these imperfect stages of the same discomycetous genus could be referred to widely separated families of the Fungi Imperfecti. In *Dermatea* a somewhat similar range of variation in the form of the conidial stroma

is found, but the conidia, themselves, are elongated to sub-filiform, while in *Pezicula* they are oblong-ellipsoid to ovoid.

The conidial stage of Dermatea molliuscula illustrates a typical Micropera. It is very similar in form to Micropera Drupacearum Lév., the conidial stage of Dermatea Cerasi (Pers.) Fries, and the type of the genus Micropera. In comparing this with a typical Cryptosporiopsis as illustrated by the conidial stages of species such as Pezicula acericola (Peck) Sacc. (Groves 1938), P. Hamamelidis Groves & Seaver (Groves 1939), P. Alni Rehm, or P. aurantiaca Rehm (Groves 1940), we find that both consist essentially of a stroma containing one or more cavities, although in Micropera the stroma is usually more erumpent and the cavities deeper and more flask-shaped. The similarity in the range of variation in the two genera can be illustrated if we compare the conidial stages of Dermatea Hamamelidis and Pezicula Rubi, D. Ariae and P. Corni, and D. Viburni and P. pruinosa. As in Cryptosporiopsis, so also in Micropera, the conidial fruiting bodies in culture tend to approach a common form consisting of a more or less globose stroma containing one or more cavities, but the conidia remain typical of those found in nature.

The genera *Dermatea* and *Pezicula* are separated chiefly on the basis of the color and consistency of the apothecia, although other differences exist such as the presence, in *Dermatea*, of a more definite epithecium and, as a rule, proportionately narrower asci and ascospores. In the conidial stages a correlation exists between these characters and the form of the conidial spore, but does not exist between them and the form of the conidial stroma. On the contrary a parallel series of variations in the form of the conidial stroma is found in both *Dermatea* and *Pezicula*. It is concluded, therefore, that the form of the conidial spore is a more stable character, and thus of greater taxonomic value than the form of the conidial stroma.

Although in the majority of species of *Dermatea* and *Pezicula* this correlation certainly exists, it does not hold for every species. The writer has previously pointed out two exceptions, *Dermatea acerina* (Peck) Rehm (Groves 1938) with apothecia like a *Dermatea* but conidia like a *Cryptosporiopsis*, and *Pezicula alnicola* Groves (Groves 1940) with apothecia like a *Pezicula* but conidia

like a *Micropera*. The question of the true relationships of these species cannot be satisfactorily answered at this time, but the writer is of the opinion that, in the present state of our knowledge of this group, it is preferable to leave these aberrant species for the time being in the genus to which they would be assigned on the basis of the characters of the perfect stage.

#### ACKNOWLEDGMENTS

The writer is indebted to Professor H. S. Jackson, Department of Botany, University of Toronto, for his continued interest and constructive suggestions; and to Dr. D. H. Linder and Dr. R. H. Wetmore, Harvard University, for their assistance in the determination of the host of the type specimen of *Cenangium subnitidum*.

CENTRAL EXPERIMENTAL FARM, OTTAWA, CANADA

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#### EXPLANATION OF FIGURES

Fig. 1. Dermatea molliuscula, A, asci, ascospores, and paraphyses, B, conidiophores and conidia; D. Ariae, C, asci, ascospores, and paraphyses, D, conidiophores, conidia, and microconidia; D. Hamamelidis, E, asci, ascospores, and paraphyses, F, conidiophores and conidia; D. Viburni, G, asci, ascospores, and paraphyses, H, conidiophores, conidia, and microconidia.

Figs. 2-13. 2, apothecia of Dermatea molliuscula; 3, apothecia of D. Viburni; 4, conidial stage of D. Viburni in nature; 5, conidial stage of D. Viburni on a twig of Viburnum in culture; 6, apothecia of D. Hamamelidis; 7, conidial stage of D. Hamamelidis in nature; 8, conidial stage of D. Hamamelidis in culture; 9, apothecia of D. Ariac; 10, conidial stage of D. Ariae in nature; 11, conidial stage of D. Ariae on a twig of Sorbus in culture; 12, conidial stage of D. molliuscula in nature; 13, conidial stage of D. molliuscula on a twig of Betula in culture. All × 4 approx.

# A NEW HOST FOR TAPHRINA BACTERIOSPERMA

W. WINFIELD RAY 1

(WITH 2 FIGURES)

Taphrina bacteriosperma Johans. was first described by Johanson (1) in 1887. He found the fungus on the leaves and stems of Betula nana L. in the Jemtland province of Sweden. In addition, he reported the fungus had also been collected in Greenland. Mrs. Patterson (2) called a fungus collected on Betula glandulosa Michx. from Mt. Washington, New Hampshire, T. bacteriosperma. Seymour (3) lists this species as occurring on B. occidentalis Hook, B. nana, and B. glandulosa. None of the collections on which this information was based was examined by the writer.

A collection of leaves of *Betula lutea* Michx., which were affected by *T. bacteriosperma*, was forwarded for study by H. S. Jackson. As far as could be ascertained, this collection represented the first time this species of *Taphrina* had been found on *B. lutea* anywhere in the world. An unnamed species of *Taphrina* has been reported affecting this host in the Plant Disease Reporter <sup>2</sup> on several occasions. The fungus in question may have been *T. bacteriosperma*.

Usually the mycelium of *T. bacteriosperma* is confined to the region of the leaf between the cuticular and epidermal layers on the lower surface, although it also may occur in a similar position on the upper side. No vegetative mycelium inhabits the inner tissues of the leaf, but, even so, the inner cells of the host are stimulated to such an extent that a hypertrophic condition results.

Infection results in definite, localized, blister-like lesions, or the entire leaf may be affected (FIG. 1). Diseased areas are concave below and convex above, and the thickness of a lesion is  $250-300 \,\mu$ , whereas, the thickness of a healthy leaf seldom exceeds  $125 \,\mu$ . The color of the diseased areas is yellow to yellowish-red.

<sup>&</sup>lt;sup>1</sup> To Dr. H. S. Jackson for his generosity in providing the material upon which this paper is based grateful acknowledgment is hereby made.

<sup>&</sup>lt;sup>2</sup> Suppl. 96: 242. 1936; 21: 34. 1939.

The asci (FIG. 2B) arise from the subcuticular mycelium and are crowded together in a compact layer. The majority of the asci are wider below than at the top, although they may be nearly cylindrical



Fig. 1. Blister-like lesions caused by Taphrina bacteriosperma on the leaf of Betula lutea, nat. size.

in some cases. Both the apical and basal ends are rounded to slightly truncate. No basal cell exists in this species.

Johanson gave the size of the asci as  $47-80~\mu$  long  $\times$   $14-20~\mu$  wide, but the writer found, as did Mrs. Patterson, that they were somewhat smaller. The asci from the collection made by Jackson were  $38-65~\mu$  long  $\times$   $14-17~\mu$  wide. The base of the ascus occasionally attained a width of  $25~\mu$ . Many small ellipsoidal spores,  $3-7~\mu$  long  $\times$   $1-2~\mu$  wide, filled the asci.

A species with which T. bacteriosperma might be confused is T. carnea Johanson. This latter fungus produces large, thickened, red, gall-like lesions on the upper surface of the leaves of various species of Betula. Its asci (Fig. 2A) are similar to those of T.

bacteriosperma in the presence of many spores in each ascus and the absence of a basal cell. However, the asci of T. carnea are longer and the bases less expanded than those of T. bacteriosperma.

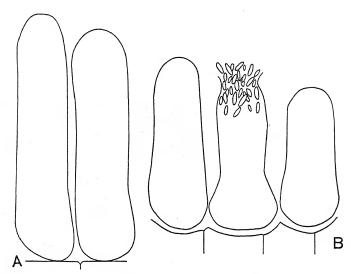


Fig. 2. A, asci of Taphrina carnea from leaf of Betula pubescens; B, asci and spores of Taphrina bacteriosperma from leaf of Betula lutea. Drawings × 893.

They are 58–80  $\mu$  long  $\times$  12–17  $\mu$  wide in the specimens studied by the writer.

Taphrina carnea is common in Europe, and it has been reported from North America on Betula glandulosa and B. nana by Seymour (3).

#### SPECIMENS EXAMINED

Taphrina bacteriosperma on Betula lutea.

Canada; Lake Temagami, Ontario, Collected by H. S. Jackson. In the University of Toronto Cryptogamic Herbarium, No. 1045. Taphrina carnea on Betula pubescens.

Norway: Kongsvell, Collected by H. H. Whetzel. In the herbarium of the Department of Plant Pathology, Cornell University, No. 23602.

#### SUMMARY

Taphrina bacteriosperma occurring on the leaves of Betula lutea in Canada is recorded on that host for the first time.

The outstanding differences in the symptoms caused by this species and *T. carnea*, and the morphological similarities and differences between the two fungi, have been discussed.

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## TWO NEW GENERA OF DISCOMYCETES FROM THE OLYMPIC NA-TIONAL FOREST 1

Bessie B. Kanouse and Alexander H. Smith (With 1 Figure)

The spring season of 1939 was spent by the junior author in the Olympic National Forest, Washington, on a mycological expedition. Among the numerous collections of Discomycetes that were made during that time are two that are here described as new. For them two new genera are erected in the family Pezizaceae. These fungi were found growing at an altitude of 5000 feet in the Hudsonian Life Zone in small areas uncovered by recently melted snow.

## Gelatinodiscus gen. nov.

Apothecia gelatinosa, mollia; stipes glaber, gelatinosus, brevis; asci cylindracei, J+; sporae ellipsoideae, leves, subflavidae; paraphyses filiformes, ramosae. Species typica, G. flavidus sp. nov.

## Gelatinodiscus flavidus sp. nov. (FIG. A-F)

Apothecia concava subexplanata vel convexa, galatinosa, mollia, flavida, 2–5 mm. lata; stipes 2–4 mm. altus, 1 mm. crassus, flavidus, levis, gelatinosus; asci cylindracei,  $150-160 \times 15-17~\mu$ , octospori, J+; sporae ellipsoideae, 2-guttulatae,  $26-34 \times 9-11~\mu$ , subflavidae; paraphyses filiformes, racemosae et curvatae. Specimen typicum legit prope Sol Duc Park, Olympic National Forest, Washington, June 20, 1939, A. H. Smith n. 14488, in Herb. Univ. of Mich. conservatum.

Apothecia solitary, stipitate, gelatinosus when fresh, drying fragile, reaching a diameter of 5 mm. opening cup-shaped, becoming convex, "yellow ochre" (R) 2 throughout, drying "dark olive," shrinking greatly on drying, hypothecium pseudoparenchymatous, exciple consisting of small thin-walled cells interspersed with groups

<sup>&</sup>lt;sup>1</sup> Papers from the Herbarium of the University of Michigan.

<sup>&</sup>lt;sup>2</sup> The colors cited in quotation marks are those of R. Ridgway, Color Standards and Color Nomenclature. 1912.

of small thick-walled cells which extend downwards into the stipe; stipe slender, measuring 2–5 mm. high and 1 mm. thick, broadly attached to the substratum; asci cylindric, thin-walled, operculate, apices turned blue with iodine, 8-spored,  $150-160 \times 15-17 \,\mu$ ; spores oblong-ellipsoid, irregularly biseriate in the ascus, contain-

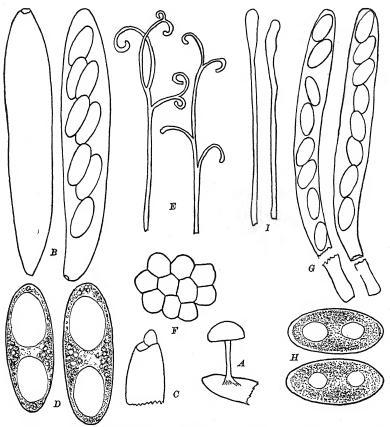


Fig. 1. A–F, Gelatinodiscus flavidus. A, sketch of mature ascophore showing convex surface of apothecium; B, mature asci  $\times$  350; C, sketch showing operculum; D, spores  $\times$  1100; E, paraphyses showing type of branching; F, sketch of hypothecial cells. G–I, P seudocollema cartilagineum. G, upper portion of mature asci; H, spores  $\times$  1100; I, paraphyses.

ing two large oil drops, smooth, greenish-yellow, 26–34  $\times$  9–11  $\mu$ ; paraphyses hyaline, slender, branched irregularly, curved and slightly enlarged at the tips, 1.5  $\mu$  thick.

On Chamaecyparis nootkatensis Sudw. lying in seepage from a

snowbank, 5000 ft. elevation, Sol Duc Park, Olympic National Forest, Washington, June 20, 1939. A. H. Smith n. 14488. Type deposited in the Herbarium of the University of Michigan.

The genus Gelatinodiscus belongs in the Pezizaceae. It is placed near Pseudombrophila although no close relationship is claimed. The operculate asci, large Peziza-like spores and the friable consistency of the dry apothecia are characters that are like those of other species placed in that family. In the fresh condition the gelatinous nature superficially allies it with the Bulgariaceae, particularly with the genus Ombrophila, but instead of drying horny as do species in that genus, or in other genera in the Bulgariaceae, Gelatinodiscus flavidus dries very fragile. On account of this characteristic it is somewhat difficult to make a microscopic mount that holds together sufficiently well for a satisfactory study. A bright yellow color exudes from the hypothecium and stains the mounting medium.

## Pseudocollema gen nov.

Apothecia coprophila, gregaria, sessilia, enascentia e cartilaginosa stromatica basi, subturbinata, mollia, catinosa; asci anguste cylindracei, J+; sporae ellipsoideae, nonseptatae; paraphyses filiformes. Species typica,  $P.\ cartilagincum$ .

## Pseudocollema cartilagineum sp. nov. (fig. G-I)

Apothecia gregaria, sessilia, enascentia e cartilaginosa stromatica basi, mollia, carinosa, aurantiaca, 1 mm. alta, 1 mm. lata; asci anguste cylindricei, 230–250  $\times$  15–17  $\mu$ , octospori, J —; sporae leves, hyalinae, nonseptatae, 19–21  $\times$  9–10  $\mu$ ; paraphyses filiformes.

Apothecia sessile, thickly gregarious, produced upon a thick cartilaginous stroma-like base formed over a dung heap, at first globose, becoming subturbinate, 1 mm. wide, 1 mm. high, soft, fleshy, bright orange throughout, fading when dry to brownish, hypothecium pseudoparenchymatous; asci cylindric, collapsing below,  $230-250 \times 15-17 \,\mu$ , 8-spored; spores smooth, hyaline, ellipsoid,  $19-21 \times 9-10 \,\mu$ , parallel or diagonally arranged; uniseriate; paraphyses slender, slightly enlarged above. Iodine does not color the asci.

On a heap of mouse dung, Deer Lake, Olympic National Forest, Washington, 5000 feet elevation, July 10, 1939. A. H. Smith n.

14992. Type deposited in the Herbarium of the University of Michigan.

The apothecia were closely gregarious upon the upper surface of a bulky, irregular, somewhat cartilaginous stromatic mass which measured 9-15 cm. long by 6-10 cm. wide and 10 cm. high. The entire mass nearly covered a heap of mouse dung that was located at the edge of a pool of ice water a short distance from a melting snowbank. The most conspicuous features of the fungus were the brilliant orange color of the apothecia and the curious stromatic mass upon which they were produced. The surface of the stroma, if that term can be applied to this structure, was uneven and wrinkled when fresh. It held its moisture content very tenaciously. Three days of continuous drying over a gasoline stove left it still somewhat rubbery. Eventually it dried down to a thin layer which does not regain its original size of color when moistened. The morphological characters of the apothecia resemble those found in species of Ascophanus. The hymenial elements are indeed so similar that without the truly remarkable stroma the fungus would be placed in that genus.

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## STUDIES IN CERATOSTOMELLA MONTIUM

MARY TAYLOR-VINJE

(WITH 30 FIGURES)

#### INTRODUCTION

For many years the genus *Ceratostomella* has been an interesting subject for investigation because of the presence, in some of its species, of the phenomenon of deliquescence of asci. Investigations of this phenomenon have brought to light several interesting observations as to the method of development in such "deliquescent type" species. The publication of two reports on the species *C. fimbriata*, one of which describes a new and unique process of ascus multiplication (2) and the other (7) typical ascomycetous development, makes it evident that further work on the "deliquescent type" species of *Ceratostomella* is desirable. The present paper reports an investigation of ascus development in a new species of *Ceratostomella* of the "deliquescent type".

#### HISTORICAL SURVEY

Because the asci are deliquescent in some of the Ceratostomellae they remained undiscovered for quite some time and led many of the early workers (4, 8, 9) to regard the fruiting body as a pycnidium; hence for many years these fungi were considered to be Fungi Imperfecti.

The first correction of this misinterpretation came when Elliott (5), finding that the fruiting body of the fungus *Sphaeronema fimbriata* contained eight spored asci, transferred the species to the genus *Ceratostomella*. He later described (6) the fungus as having a development similar to that found by Harper in *S. Castagnei* except that no croziers were found to initiate ascus formation in *C. fimbriata*.

Sartoris (12) corrected another taxonomic error when he showed that *Sphaeronema adiposum* was, like *C. fimbriata*, an ascomycete belonging to that same genus; he renamed the fungus *Ceratosto*-

mella adiposa. His description of the development in the fungus is especially interesting because it reports a complete absence of sex organs or cell fusions as well as the formation of asci without the intervention of croziers.

Varitchak (13) in a study of *C. Piceae* was the first to report the presence of croziers in a "deliquescent type" species of *Ceratostomella* though he called attention to the fact that such structures are figured though not reported in the work of Elliott (6).

Reports of both the presence and absence of croziers brought renewed interest in the genus, especially in the species *C. fimbriata* upon which most of the subsequent work was done.

Mittmann (10) confirmed Elliott as to the absence of croziers in ascus formation in *C. fimbriata* and further reported that all nuclear divisions in the ascus are confined to a central zone and that the ascus lacks a wall until maturation of the spores.

Andrus and Harter (2) confirmed Mittmann as to the absence of croziers and as to the unwalled condition of the asci in *C. fimbriata*. They further reported that the first nuclear division is characterized by the development of a distinct ascus vesicle which, they suggest, seems to be the membrane of the fusion nucleus. They consider that all three nuclear divisions, as well as delimitation of the ascospores, occur within this vesicle. Andrus and Harter further maintain that this vesicle expands during nuclear division and, by the time the spores are formed, becomes the wall of the ascus. Andrus and Harter are the first workers to report the wall of a fusion nucleus becoming the wall of an ascus, and they suggest that "The procedure is doubtless peculiar to those species of Pyrenomycetes whose asci in their younger stages are without a definite wall." <sup>1</sup>

A study by Andrus (1) of *C. multiannulata* reported a development very similar to that found in *C. fimbriata* (2) except that there was never any indication of an ascus vesicle or an endogenous ascus wall although it was noted that spore formation was restricted to the central region of the ascus.

At a later date, in a more intensive study of the ascus development in C. fimbriata and C. moniliformis, Andrus and Harter (3)

<sup>&</sup>lt;sup>1</sup> Andrus and Harter: Morphology of reproduction in *Ceratostomella fimbriata*. Jour. Agr. Res. 4: 1059-1098. 1933.

confirmed and extended their earlier views. They came to the conclusion that, in the initiation of asci, not only direct and indirect types of cleavage but also the typical crozier type of cleavage may take part. In both species they found the fusion nucleus to consist of a chromatin network with a nucleolus. In the first division in the ascus of C. moniliformis two bilobed (or perhaps four distinct) chromatin bodies were observed on the spindle; in C. fimbriata two comma shaped and two bilobed chromatin bodies were found. No reduction division occurred in the ascus according to these authors. No endogenous ascus wall, such as had been previously reported for C. fimbriata (2), was found in C. moniliformis although a cleavage in the cytoplasm, corresponding in position to the margin of the nuclear vesicle of C. fimbriata, was observed. Ascospore formation was observed to occur in a most peculiar manner there being apparently no evidence of astral radiations or free cell formation.

Gwynne-Vaughan and Broadhead (7), in a study of the oft investigated C. fimbriata, contrary to the findings of Andrus and Harter (2), observed a typical ascomycetous development. They failed to confirm the absence of ascogenous and ascus walls as reported by Andrus and Harter (2) and could find no evidence of the ascus vesicle figured by Andrus and Harter (2) and Mittmann (10) in the ascus. Asci were observed to develop by typical crozier formation and three was observed to be the haploid chromosome and the gemini number.

From the above discussion it is evident that there exists at present much controversy as to the type of development found in those species of *Ceratostomella* which have deliquescent asci. While it is entirely conceivable that different species within the same genus may have different types of development it is hardly probable that an individual species would show such variance in its development as would be indicated by the reports made for *C. fimbriata* (2, 3, 6, 7, 10). Such controversy over one species makes it evident that an investigation of a new species of *Ceratostomella* may well be of interest.

#### MATERIALS AND METHODS

Ceratostomella montium Rumbold was used in this investigation. The fungus had been isolated by Dr. Caroline Rumbold <sup>2</sup> from beetle galleries occurring in lodgepole pine (Pinus contorta Loudon). The trees were obtained from a forest on Elk Mountain, Carbon County, Wyoming. The fungus causes a blue stain in the trees and is associated with Dendroctonus ponderosae Hopkins and D. monticolae Hopkins. The fungus was named and described by Rumbold (11).

The fungus was cultured in petri dishes on a medium consisting of a 4.15 per cent corn meal decoction and 1.5 per cent agar. On this medium mycelial growth was fairly scant and the perithecia readily visible. A constant temperature of 21° C. was used.

Several fixatives were tried but Flemming strong diluted one half with distilled water and Bouin's (Allen's modification) proved to be most satisfactory. The fixative employed was poured directly into the petri dish containing the culture as soon after its removal from the incubator as was possible.

Fixations were made twice a day from the third to the twelfth day of growth, when the perithecial necks were just beginning to elongate, at which time fixations were made every hour for a twenty-four hour period and then daily again until the perithecia were mature.

Following fixation, washing, and dehydration, butyl alcohol was used as the paraffin solvent and the material was embedded in a mixture of commercial Parowax and crude rubber  $^{8}$  and cut at 1  $\mu$  to 15  $\mu$  in thickness. 7  $\mu$  was found to be most satisfactory.

As a stain Heidenhain's Iron-Alum Haematoxylin gave the most satisfactory results. When counterstained, erythrosin was used. Triple stain was found to be inferior to Heidenhain's stain for this fungus.

Temporary mounts for supplementary study of all stages, from perithecial initials to crushed mature perithecia containing ascospores, were made in lactophenol and cotton blue.

<sup>&</sup>lt;sup>2</sup> Division of Forest Pathology, Bureau of Plant Industry, in coöperation with the Forest Products Laboratory, Madison, Wis.

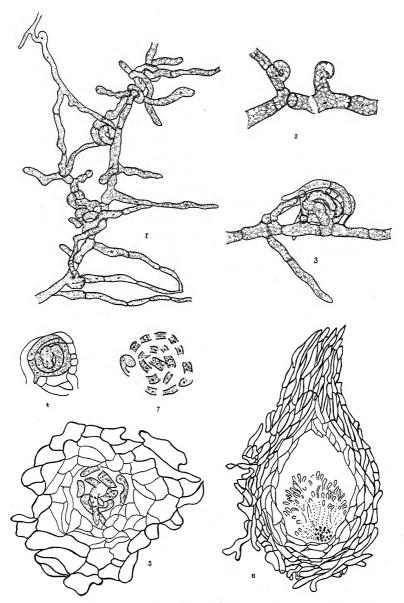
<sup>&</sup>lt;sup>3</sup> Stock—20 grams crude rubber and 100 grams Parowax. Use 5 grams stock with 100 grams Parowax for embedding.

## MORPHOLOGY AND CYTOLOGY OF THE PERITHECIUM IN CERATOSTOMELLA MONTIUM

The primordia of the ascocarps which give rise to perithecia may be recognized, microscopically, in culture, within forty-eight hours. The perithecia develop in small groups scattered about the plate and within seven days are visible to the naked eye. Within twelve days some of the perithecia can be seen to be maturing and, with a microscope, the beginnings of short necks are visible. Such perithecia usually produce long necks by the end of the month. It is to be noted that with the appearance of such maturing perithecia those immediately adjacent in each group cease development. It seems possible that such abortion may be related to food supply. It might be further pointed out that wherever large numbers of perithecia are produced there are frequently found sclerotial-like bodies having a slimy grey appearance. Microscopically these are seen to be composed of numerous tiny conidial-like spores. These spores differ, however, from the true conidia both in size and manner of production. The relation between these "microconidia" and perithecial production was not determined.

A perithecium originates as a short recurved branch on one of the vegetative hyphae (Fig. 2). No evidence of an antheridium has ever been encountered. The recurved branch continues to coil but soon becomes enveloped by branches which arise from adjacent cells (Fig. 3) forming a small knot. Several such knots usually develop in a series on any one hypha and occasionally such knots have been observed to end in long narrow cells which, at least superficially, resemble trichogynes (Fig. 1).

Each small knot consists of a sterile outer sheath and an inner fertile coil, the latter being derived from the enlargement and curvature of the original short recurved branch. The tip cell of the fertile coil is binucleate (FIG. 4). The origin of the binucleate condition was not determined. The coil soon becomes multinucleate (FIG. 7) through nuclear divisions not followed by cell divisions and from this coil there arise multinucleate ascogenous hyphae (FIG. 5). In most cases, with the development of the ascogenous hyphae, the coil is used up and, for this reason, the asci seem to come directly from the walls of the perithecium.



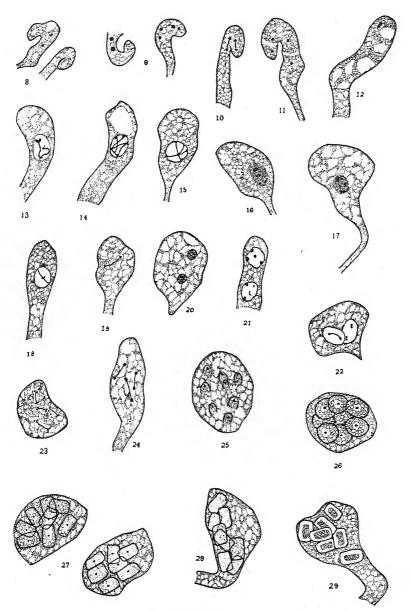
Figs. 1-7.

However, the presence of a coil (FIG. 6, 7) at the base of a perithecium in whose cavity the ascogenous hyphae are producing asci suggests that certain cells of such a coil may well be the origin of the ascogenous hyphae.

Coincident with the development of the ascogenous hyphae there has been the development of a sterile sheath. The cells of the hyphal branches which had first enveloped the young coil increase in number, enlarge, and fuse so as to form a sheath of two layers about the coil (FIG. 5). The peripheral layer consists of dark brown, thick-walled cells which form a tough outer perithecial wall. The inner layer is pseudoparenchymatous in nature consisting of thin-walled, colorless cells. Occupying the central cavity of the perithecium lies the fertile coil embedded in a mass of thinwalled, cushion-like cells. These cushion cells break down readily coincident with the maturation of the fertile coil; it is assumed that the cushion cells perform a nutritive function. It is interesting to note that the cells of the outer brown sterile jacket frequently produce conidia, so that small clusters of conidia are commonly found around the perithecia. Small round cells identical in appearance with the conidia have been observed within the perithecial cavity, usually at the periphery. The vegetative hyphae which form the perithecial wall have apparently retained the capacity to produce conidia.

Within the perithecium the ascogenous hyphae begin the production of asci in typical fashion by the formation of croziers. The hyphae extend upward into the cavity, developing at the expense of the cushion cells, and spread out to partially fill the cavity in a somewhat bouquet effect (FIG. 6). The tips of these ascogenous hyphae are frequently seen to curve in typical crozier formation (FIG. 8–11). In these croziers, which are binucleate, nuclear divisions to form four nuclei have been observed (FIG. 10, 11). Two cross walls are then laid down which cut off a binucleate penultimate cell which develops into the primary ascus (FIG. 11, 12). In this young ascus a nuclear fusion occurs, and following this fusion the ascus enlarges considerably and is seen to contain the characteristic single, large primary nucleus (FIG. 13–15).

The primary nucleus of the ascus consists of chromatin material which strings across the central part of the nucleus and ends in



Figs. 8-29.

small aggregations at the periphery (FIG. 13-15). In the prophases of the first division there are differentiated either four or six chromatin masses. The chromatin aggregations are so arranged that they may be interpreted either as six very small bodies, two pair of which are very close together, or as four bodies, two of which are bilobed (FIG. 16, 17). Following the first division (FIG. 18, 19) two nuclei are formed (FIG. 20) which undergo a second (Fig. 21, 22) and third division (Fig. 23, 24) to form eight nuclei. Such stages occur in rapid succession and are difficult to find; the uninucleate stage is the prolonged one. The small size of the chromatin masses made counts in the second and third divisions impossible. Following the production of eight nuclei, free cell formation occurs (FIG. 25). Because of the minute size of the nuclei the writer was unable to determine whether the nuclei were beaked or not. The spores are round when first cut out (FIG. 26) but later become polyhedral in shape (FIG. 27). Some of the ascus cytoplasm seems to remain as flanges on the spores. The spores are not subjected to much pressure within the ascus but rather lie free within that structure (FIG. 28). They readily undergo contraction and as a result often seem to consist of a narrow bar of protoplasm surrounded by a very thick transparent wall (Fig. 29); but in other cases they are seen to be well filled with protoplasm (FIG. 27). The ascus wall is very thin and, coincident with the enlargement of the ascospores, deliquesces leaving the spores lying free within the perithecial cavity (Fig. 30). Some enlargement of the spores occurs after their liberation from the ascus.

At some time previous to the production of the asci the pseudo-parenchymatous cells in the upper part of the perithecium are seen to be growing. They turn upward and begin to elongate, pushing aside the outer sheath, which, however, is itself still capable of some growth in that region. These rows of elongate, narrow cells resemble an aggregate of vegetative hyphae. They continue to elongate ultimately forming a long neck. The outer hyphae of the neck resemble those of the outer layer of the perithecial wall being of the same dark brown color and having thick-walled cells. The inner hyphae consist of thin-walled hyaline cells like those of the pseudoparenchyma of the perithecium. By the time the

ascospores are mature the neck has reached its full length. The central hyaline cells then break down leaving a long central canal (Fig. 30). The perithecium now imbibes water and its contents begin to swell. A pressure is exerted which forces the perithecial contents up the canal of the neck and out of the ostiole. The disintegrated cells of the neck as well as some of the cellular remains of the perithecial cavity tend to hold the ascospores together in a sticky droplet at the tip of the neck.

#### DISCUSSION

Perithecial development in *C. montium* agrees in many respects with that in other species of this same genus. Although Varitchak reports the presence of an antheridium in the lumber blue stain fungus *C. Piceae* (13), it is to be noted that he considers it nonfunctional, and that he believes the ascogone originates as a binucleate structure; Andrus and Harter report a similar situation for the antheridium in *C. fimbriata* (2) whereas Gwynne-Vaughan and Broadhead (7) do not recognize even a non-functional antheridium. If the absence of an antheridium is to be considered an indication of reduction, then *C. montium* is certainly more reduced than *C. Piceae* and at least as reduced as *C. fimbriata* since it shows no evidence of an antheridium.

The origin of the binucleate condition in *C. montium* was undetermined. The fact that large numbers of perithecia are usually accompanied by the production of the aforementioned sclerotial-like bodies should not be lost sight of in the matter of possible explanations for such a binucleate condition. However, since there is at present no evidence to account for this binucleate condition, it is suggested that possibly in this species, as has been described for *C. Piceae* (13) and *C. fimbriata* (7), the binucleate condition arises as a result of a nuclear division not followed by septation.

C. montium resembles the other species of this genus in that the young fertile coil early becomes enveloped by a sheath resulting from the branching and fusion of hyphae which arise from cells adjacent to those which form the coil.

The multinucleate condition of the ascogenous hyphae presumably arises, as described in C. fimbriata (7), C. Piceae (13), C.



Fig. 30.

adiposa (12), and C. multiannulata (1), by a series of nuclear divisions not followed by cell divisions. Although the ascogenous hyphae seemed to present a naked condition as described by Andrus and Harter for C. fimbriata (2) and by Andrus for C. multiannulata (1), the presence of a wall in later stages of development

led the writer to assume that such apparently unwalled condition was due to protoplasmic contractions as suggested by Gwynne-Vaughan and Broadhead (7) for *C. fimbriata*.

In regard to the method of ascus formation *C. montium* agrees with those species in which typical crozier production has been described (7, 13). However, since there still seems to be some question as to whether crozier formation is the only method of ascus initiation in *C. fimbriata* (3), it may be that although typical croziers have now been reported in two of the blue staining members of the genus, in *C. fimbriata* (3) and in some of the other species (1, 2, 3) these stages have been somewhat modified.

Development within the ascus is of a typical ascomycetous nature. The three divisions appear normal. The number and appearance of the chromatin bodies resemble that found by Andrus and Harter in *C. fimbriata* (3). In no case was there any evidence of an ascus vesicle as described by Andrus and Harter for *C. fimbriata* (3); nor was the apparently naked condition of the asci as described for that same species and for *C. moniliformis* (3) and *C. multiannulata* (1) ever observed in *C. montium* although contractions of the cytoplasm often seemed to indicate that such was the case. Destaining to the point where nuclear structure was discernible often made both cytoplasm and wall very faint, especially when Heidenhain's Haemotoxylin stain, which is essentially a nuclear stain, was used. As has been pointed out by Gwynne-Vaughan and Broadhead (7) well fixed and well stained preparations show the cytoplasm and wall to be normal.

Ascospores are produced in *C. montium* by typical free cell formation. No evidence of their developing as protuberances on a central protoplasmic mass, as described by Andrus and Harter (3), for *C. fimbriata* and *C. moniliformis* has ever been encountered. However, as described for those and other species of this genus (1, 2, 3, 7, 12, 13) the ascus wall of *C. montium* deliquesces early, frequently even before the spores have reached their mature size.

Although the development of the neck in *C. montium* was not followed in detail it follows in general that so adequately described by Sartoris for *C. adiposa* (12). As in *C. Piceae* (13) the outer cells of the perithecial wall of *C. montium* give rise to the outer cells of the neck.

In the liberation of its ascospores *C. montium* agrees with the condition found in *C. Piceae* (13) and *C. fimbriata* (7). As in other species of this genus (7, 12, 13) the ascospores are emitted in a gelatinous mass.

In conclusion the information concerning this new species of Ceratostomella might be summarized as follows. In respect to sex organs C. montium is less primitive than C. Piceae (13), C. fimbriata (2) (except according to the Gwynne-Vaughan and Broadhead (7) interpretation) or C. multiannulata (1) but perhaps not as reduced as C. adiposa (12) in that there is no antheridium but there is found a recurved initial comparable to an oögonium. In the development of its asci C. montium resembles especially C. Piceae (13) being similar in the production of croziers, neck formation, spore delimitation, and spore liberation. In "chromosome" number C. montium resembles C. fimbriata (3).

In general, from the foregoing observations, it would seem that *C. montium* is a typical ascomycete in its development.

#### SUMMARY

The fungus was cultured in petri dishes on a medium consisting of 4.15 per cent corn meal decoction and 1.5 per cent agar at 21° C.

The ascospores are produced in dark brown perithecia which have long necks from whose tips the spores are extruded as a gelatinous mass.

The perithecia often develop in groups but only a few of any one group ever mature.

Normal perithecial initials are visible, microscopically, in four to seven-day old cultures. Uninucleate asci begin their development within twelve days and perithecia mature within a month.

The perithecium begins as a recurved branch. No antheridium has ever been observed.

The recurved branch coils on itself and becomes the fertile coil of the young perithecium.

Cells immediately adjacent to those producing the fertile coil give rise to the sterile sheath.

The cells of the fertile coil become multinucleate by nuclear divisions not followed by cell divisions.

Some cells of the fertile coil give rise to ascogenous hyphae at whose tips asci are formed by typical crozier development.

Asci are produced successively by the ascogenous hyphae.

The primary nucleus of the ascus shows strands of chromatin material which tends to aggregate at the periphery of the nucleus.

In the prophases of the first division either four or six chromatin aggregations are visible.

Within the ascus three nuclear divisions produce eight nuclei about which spores are delimited by free cell formation.

The spores are round when first cut out but they later take on a polyhedral shape bearing flanges which seem to be cytoplasmic remnants.

Coincident with, or shortly before, the time the spores reach their full size the ascus wall disappears leaving the spores lying free in the perithecial cavity.

The perithecial sheath consists of two zones—an outer layer of dark brown, thick-walled cells and an inner pseudoparenchymatous layer of thin-walled cells.

At the time the ascogenous hyphae are developing beak formation begins. By the time the ascospores are mature this beak has elongated into a neck whose inner cells break down to allow for the escape of the spores.

#### ACKNOWLEDGMENTS

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#### EXPLANATION OF FIGURES

Figs. 1–29. Drawings were made with the aid of a Spencer camera lucida at table level. Reduction of all figures ca. 1/3.

Fig. 1, young perithecial knots (ca. × 520); 2, perithecial initials (× 1040); 3, young fertile coil being enveloped by sheath hyphae which are developing from adjacent hyphal cells (× 1040); 4, cross section of young knot containing binucleate tip cell and showing multinucleate condition of rest of coil. Sheath cells are at periphery (× 1460); 5, multinucleate ascogenous hyphae which have developed from the fertile coil. Sterile sheath shows considerable development (× 1040); 6, young perithecium in which asci are being formed in the center of the cavity. At the base is a persistent fertile coil. Opposite the coil is the elongating neck. The perithecial sheath shows two zones (× 220); 7, enlargement of the fertile coil observed at the base of the perithecium shown in Fig. 6 (× 1040).

Figs. 8-29. All drawings are  $\times$  1860. Figs. 8-11, stages in crozier formation; 10, division in the crozier to form four nuclei; 11, four nucleate crozier; 12-15, primary asci; 13-15, nuclei of primary asci showing arrange-

ment of chromatin material; 16, 17, prophases of the first division showing chromatin aggregations which may be interpreted either as six very small bodies or as four, two of which are bilobed; 18, 19, first nuclear division in the ascus; 20, binucleate ascus; 21, prophases of the second nuclear division in the ascus; 22, second nuclear division in the ascus; 23, 24, third nuclear division in the ascus; 25, free cell formation in the ascus; 26, spores as cut out in the ascus are, at first, round; 27, spores becoming polyhedral; 28, spores lying free in the ascus—show no evidence of pressure; 29, spores in the ascus showing the peculiar bar of protoplasm due to contraction.

Fig. 30. Photomicrograph. Longitudinal section through mature perithecium showing cavity filled with polyhedral ascospores. The thick walled sheath can be seen at the periphery and at the top is the neck with its open canal. ca. × 250.

# THE GENUS ARMILLARIA IN WESTERN WASHINGTON

H. H. Hotson

(WITH 3 FIGURES)

The genus Armillaria is well represented in western Washington, some species occurring very abundantly, especially Armillaria mellea. The genus was first recognized by Fries in 1821 (4) as a tribe under Agaricus but later it was discarded by both Ricken and Lange who distributed the species among other genera. In 1914, Ricken (23) in his reorganization of the genus, transferred seven species, including Armillaria mellea, to the genus Clitocybe, nine to Tricholoma, three to Collybia, and four to Pleurotus. In 1914, Lange (18) in general followed Ricken's interpretation of the genus but placed Armillaria mellea in the genus Lepiota.

In America most mycologists have not accepted this abolition of the genus for, although admitting it to be a more or less heterogenous group, they believe that transferring the various species to other genera does not solve the problem. Peck (21), in 1890, describes eight species which, at that time, were known in the United States. Murrill (20), in 1914, listed 14 species, two of which were tropical. He only included three of Peck's eight and left the others unmentioned. Kauffman (13), in 1918, described six species, two of which, A. dryina and A. corticata, had previously been placed in the genus *Pleurotus*. Again, in 1922, he (15) consolidated the genus for the United States and listed 28 species, eleven of which have been reported for Washington and Oregon, and two of which have later, due to the work of Zeller, been proven to be synonymous, A. ponderosa and A. arenicola (27). Since that time five additional species have been reported by Zeller and Kauffman for Washington and Oregon. In the present article, which is the fourth of a series on the Agaricacae of Western Washington (10, 11, 12), fifteen species are reported.

The writer has two main objects in view in this article: to bring

together the scattered information regarding the genus as it occurs in the Pacific Northwest; and to put this and any new information into a usable form so that it may be a basis for further study of the genus. To this end a key has been constructed similar to that given in another article (12), which combines the usual skeleton key with a more or less complete description of each species in order to facilitate their identification.

There is some difference of opinion among mycologists as to the exact limits of this genus. Certain species seem to be transitional forms having certain characteristics of Armillaria and others of the genus Lepiota. Armillaria is described as having an annulus and attached gills, and Lepiota an annulus and free gills. A. granosa and A. amianthina (which were formerly placed in the genus Lepiota) have an annulus and attached gills, while in other respects they are like Lepiota. Kauffman quite logically has transferred such forms to the genus Armillaria and in this paper his interpretation has been accepted. There are a few species, such as A. dryina and A. corticata, commonly placed in the genus Pleurotus because of their eccentric or lateral stems, which have a ring and the gills attached or decurrent. Following Kauffman's suggestion, these have been placed in the genus Armillaria, also. Thus, any white-spored form with attached or decurrent gills, with the stem and pileus continuous, having a ring but lacking a volva, is considered to belong to the genus Armillaria.

ARMILLARIA Fries, Syst. Myc. 1: 26. 1821

(From the Latin, armilla, a ring, referring to the presence of the annulus)

Pileus fleshy, regular; gills adnexed, adnate or decurrent, sometimes with a diverging trama; stem fleshy, continuous with the pileus, central or lateral; annulus present, persistent, membranous or subarachnoid; spores white in mass, smooth; growing on the ground or on wood, mostly in the autumn; often compact, firm mushrooms; sometimes caespitose.

In structure this genus resembles *Pholiota* among the ochraspored, and *Stropharia* of the purple-brown-spored species.

### KEY TO THE SPECIES OF ARMILLARIA

- A. Stem lateral or eccentric; pileus white or whitish.
  - B. Spores oblong 9-10 × 4-4.5 μ, smooth and white; gills not anastomosing at stem, decurrent, white, broadest in the middle; pileus white, 4-8 cm. broad, firm, floccose at first, becoming scaly from the breaking up of the floccose covering, scales darkening with age, margin at first involute; stem lateral or eccentric, 2-4 cm. long, 1-1.5 cm. thick, sometimes becoming densely hairy, especially toward the base; annulus somewhat evanescent; veil thin and membranous; ador strong of bitter almonds.
    1. A. dryina (Fries) Pat.
  - BB. Spores cylindrical 13-17 × 4-5 \( \mu\), smooth and white; gills anastomosing at the stem, decurrent, narrowed toward the stem, white becoming yellowish, edge entire; pileus 6-15 cm. or more broad, convex-expanded, obtuse or depressed, firm, dull white or becoming brownish, finely floccose at first, cuticle breaking up into scale-like areas, margin involute at first; stem 4-10 cm. long, eccentric, sometimes stout and short, solid, firm, subtomentose or floccose, reticulate in large specimens; annulus thin, white floccose-membranous, evanescent; odor disagreeable.

    2. A. corticata (Fries) Pat.
- AA. Stem central or nearly so.
  - C. Gills decurrent, sometimes adnate, whitish or dingy yellow, becoming rusty with age, often powdery white due to the spores; pileus 3-10 cm. or more broad, oval, becoming convex to almost plane, usually honey-colored, varying to yellowish-brown or pale covered with dark-brown or blackish pointed scales, margin striate in age, context white; stem variable in length, 5-15 cm. long, 6-20 mm. thick, equal, stuffed becoming hollow, elastic, floccose scaly, whitish above, dingy yellow, brownish or rusty-stained below; annulus superior; veil usually well developed, membranous, both veil and annulus sometimes evanescent; spores elliptical-ovate, 8-9.5 × 5-6.5 \mu, white, smooth, nucleate; taste somewhat disagreeable or acrid.

    3. A. mellea Fries.
  - CC. Gills variously attached but not decurrent (exc. A. granulosoides sometimes)
    - D. Pileus granulose or granulose-warty
      - E. Gills adnate
        - F. Disc of the pileus rugose
          - G. Growing on rotten wood or stumps; pileus 5–9 cm. broad, ovate, then convex-expanded, umbonate or obtuse, ochraceous to cinnamon-brown, furfuraceous-granulose, rugose-wrinkled to almost even, margin regular or undulate, context thick, white or slightly ochraceous; stem 5–10 cm. long, 8–15 mm. thick, equal or tapering upward from the clavate base, peronate by furfuraceous or floccose scale, colored like the pileus; annulus membranous, large, flaring, persistent; gills crowded, adnate, sometimes subarcuate, whitish to ochraceous; stores smooth, 4–5 × 3 μ. 4. A. granosa Kauff.

- GG. Growing on the ground; pileus 1-4 cm. broad, rugose-reticulate, cinnamon-brown on the disc, antimony-yellow to ochraceous on the margin, not umbonate, context thick and white; stem 4-7 cm. long, 3-4 mm. thick, equal or tapering upward, solid, peronate with cinnamon or reddish-brown floccose scales; gills adnate, sometimes subdecurrent, crowded, white, edge entire; spores 4-5.5 × 3 μ, smooth, ovoid, apiculate, white; annulus incomplete or evanescent.
- 5. A. rugoso-reticulata Zeller. FF. Pileus not rugose, 2-6 cm. broad, ovoid to campanulate and convex-expanded, subombonate, surface finely to coarsely granulose, ochraceous to reddishferruginous varying to pallid or pinkish, context thin, white or yellowish; stem subequal, 4-8 cm. long, 2-7 mm. thick, whitish at the apex, covered with ochraceous granules below the annulus; annulus membranous, large; veil lacerate more or less appendiculate; gills adnexed to adnate, at times apparently free, rather broad, close, white becoming yellowish; spores 3-7 × 2.5-4 µ, elliptical or subglobose, smooth, white; odor disagreeable.

  6. A. amianthina Kauff.

#### EE. Gills adnexed

H. Pilieus ochraceous or rusty-brown becoming paler when dry, 3-6 cm. broad, ovate becoming convex-expanded, or subumbonate, furfuraceous-granular, often radiately wrinkled, context thin, yellowish white becoming reddish; stem 2-5 cm. long, 4-8 mm. thick, stuffed to hollow, equal or tapering upward, granulose to floccose-scaly and reddish below the annulus, whitish at the apex; annulus slight, evanescent; gills adnexed, rounded at the stem, white; spores 4-5 × 3-3.5 μ, ovate, smooth; cystidia none.

7. A. granulosa Kauff.

HH. Pileus cinnabar-red or rusty red, 5-8 cm. broad, convex to plane, obtuse, furfuraceous-granulose, margin fimbriate, context ochraceous, reddish under the cuticle of the pileus and stem; stem 4-7 cm. long, 1-2 cm. thick, equal or tapering upwards, covered with reddish granules below the ring; gills white, adnexed, sometimes nearly free; annulus concolorous, thin, narrow, inferior, evanescent; spores white, elliptical, obtuse, 4 × 2.5-3 μ, one-guttulate; cystidia hair-like, acute.
8. A. cinnabarina Kauff.

#### DD. Pileus not granulose or granulose-warty

#### I. Pileus 2-6 cm. Broad

J. Spores 3-4.5 × 2-3 \( \mu, \) elliptical, white, often adhering in groups of two, three, or four; pileus 2-5 cm.

broad, convex, expanding to plane and usually depressed in center, surface squamulose scaly, light ochraceous-buff to tawny, sometimes staining almost russet, cream to buff between the scales, context thin, white, to creamy; stem 2–5 cm. long, 2–4 mm. thick, rufescent to tawny above and below, peronate with floccose to subfloccose scales; gills broad, adnate to slightly decurrent, often breaking away, white to creamy, edges even; annulus superior, thin, small, evanescent.

- 9. A. granulosoides Zeller.
   JJ. Spores 5.5-7 × 5-6 μ, oblong to subglobose, white; pileus 4-6 cm. broad, convex to plane, slightly umbonate, surface dry, squamulose on disc to fibrillosescaly toward margin, bay to brown on the disc, to light ochraceous-salmon towards the margin, context rather thin at margin, thick at the disc, white to creamy, slowly becoming pinkish when exposed; stem hollow, 5-7 cm. long, 8-12 mm. thick, striately fibrillose scaly; gills white, becoming pinkish, adnate, edges even; annulus fugaceous, arachnoid; odor and taste slightly farinaceous.
   10. A. badicephala Zeller.
- 11. Pileus usually much larger
  - K. Pileus white, creamy-white or buff; not with marked yellow or red shades
    - L. Odor strong, penetrating, subalkaline; spores ellipsoidal, 5-6 × 3-3.5 μ; pileus fleshy, 6-15 cm. broad, compact, convex to plane, glabrous, whitish with a slight yellowish or reddish-yellow tint, margin at first incurved and tomentose, context compact, white; stem equal, 4-10 cm. long, 2-3 mm. thick, solid, firm, sheathed at first with a thin membranous veil; gills narrow, crowded, sinuate, adnate or subdecurrent, whitish; annulus whitish above, narrow, membranous, more or less flaring.
      11. A. viscidipes Peck.
    - LL. Odor mild; spores white, smooth, subglobose to oblong,  $5-6 \times 4.5-5 \mu$ ; pileus 8-21 cm. broad. thick, firm, convex or broadly umbonate to gibbous, nearly plane when expanded, dry to subviscid, glabrous becoming fibrillose, at first white or pinkish buff, disc becoming light ochraceous-salmon, margin white to creamy, inrolled, context white, firm; stem 10-15 cm. long, 3-4 mm. thick, cylindrical or tapering downward, smooth below, somewhat scaly above the annulus; gills emarginate, becoming sinuateadnexed or breaking free at maturity, whitish to light buff becoming warm buff, changing to brown when bruised; annulus ample, persistent, membranous. 12. A. ponderosa (Peck) Sacc.

KK. Pileus with marked yellow or red shades

M. Pileus apricot-yellow to yellowish brown, darker at the center, viscid, 5-10 cm. broad, tinged tawny in age, convex to expanded, umbonate, margin thin, slightly repandent, smooth; stem 6-8 cm. long, 8-12 mm. thick, straight, even, stuffed-hollow, coarsely floccose, woolly up to the annulus, white, smooth above; gills thin, sinuate-adnate to adnexed, white becoming pale yellow; spores white, smooth, subelliptical, 4-6 × 3-4 µ; veil present when young, persisting as an inconspicuous annulus.
13. A. albolanaripes Atk.
MM Pileus with reddish brown or reddish.

MM. Pileus with reddish-brown or reddishorange shades

N. Pileus covered with tawny-orange to ochraceous-rufous scales, 5–7 cm. broad, convex then expanded, subumbonate, with a pellicle which soon breaks into numerous crowded scales, margin at first inrolled and glutinous-floccose, context white, thin on the margin; stem 4–7 cm. long, 8–15 mm. thick, solid, equal or tapering downward, covered by concolorous scales up to the evanescent annulus, white at apex and between scales; gills rounded near the stem, slightly adnexed, white, spotted rusty-brown in age, some forked, edge entire; spores globose-oval, variable, 4–5 × 3–4 μ, smooth, nucleate, white; odor strongly farinaceous, somewhat disagreeable.

14. A. aurantia Fries.

NN. Pileus glabrous (sometimes innate-fibrillose), compact rimose, viscid when wet, 7-15 cm. broad, margin somewhat revolute, undulate at maturity, and slightly exceeding the gills, disc ochraceous-tawny to brown with orange spots, a light pale-tan toward the margin, context white, thick at the disc; stem cylindrical or tapering downward, 6-15 cm. long, 1.5-3.7 cm. thick, scaly below, squamulose above, creamy, stained reddishbrown where bruised; gills 1 cm. broad, whitish becoming ochraceous-tawny at maturity, drying various shades of buff, darker where bruised, edges entire to wavy; annulus superior, fibrose-membranous; spores ellipsoid to ovoid,  $6-7.5 \times 3.5-5 \mu$ , white.

15. A. robusta (Alb. & Schw.) Fries.

#### DISCUSSION

Armillaria dryina (Fries) Pat. Tax. Hymén. 156. 1900.
 Syn.: Pleurotus dryinus Fries, Syst. Myc. 1: 180. 1821;
 Hymen. Eur. 167. 1874.

Although this species has been reported in eastern United States occurring on stumps and logs, the collections in Washington have been mainly in the ground in wet ravines. As suggested by Kauffman (15), this might account for the unusual tomentose character of the stem. It has the general appearance of *Pleurotus* in which genus it was formerly placed, but with the present conception of the genus *Armillaria* it should logically be placed in that genus. It is characterized by a strong odor of benzaldehyde (bitter almonds) and has a flat unpleasant taste.

Collected in a ravine near Richmond Beach, Oct. 15, 1939.

A. corticata (Fries) Pat. Tax. Hymén. 156. 1900.
 Syn.: Pleurotus corticatus Fries, Syst. Myc. 1: 179. 1821;
 Hymen. Eur. 166. 1874.

This species was first found in the Pacific Northwest in Oregon by S. M. Zeller in 1922 (25). It is not common. I have not been able to find any in the field but have had access to specimens in the herbarium. This species has an eccentric stem resembling *Pleurotus*, but as it has a ring with the pileus and stem continuous, and the spores white, it has been placed in the genus *Armillaria*. It is very similar to *A. dryina* and Atkinson (1, p. 106) has considered it merely as an ecological form. Kauffman, however, found a difference in the size of the spores and considered it a separate species. Schroeter gives the size of the spores as  $13-15 \times 4-5 \mu$  and our herbarium specimens come within that range.

3. A. mellea Fries, Syst. Myc. 1: 30. 1821.

This species is very common around Puget Sound and is the most outstanding one of the entire genus. It has no close relation to any other form and can readily be recognized by the decurrent gills. It is often known as the "Honey Mushroom," and the "Honey Agaric" on account of the yellowish pileus. It is extremely variable in its characters and seems to combine some of

the features of many of the Agarics. It is of economic importance in that it causes a root rot of both trees and shrubs in the forest and in the orchard. The fungus which attacks conifers does not seem to attack fruit trees and vice versa, suggesting that there are two strains of mycelia. However, no distinction in the sporophores can be seen. It is found in caespitose clusters at the base of living trees and is parasitic on the roots. It forms very pronounced rhizomorphs which are easily found in the immediate vicinity of the sporophores.

The rhizimorphs have been found very abundant in certain wells in the vicinity of Seattle forming mats of intertwining black threads in the water. They have also been found in masses hanging from decaying timber supports in mines. An examination of these rhizomorphs in relation to the plants which they attack indicates that they are capable of gaining entrance to the host by a sort of mechanical pressure rather than by an enzyme.

4. A. granosa (Morg.) Kauff. Papers Mich. Acad. Sci. 2: 60. 1922.

Syn.: Lepiota granosa Morg., Myc. Flora Miami Valley 2: 63.

The umbo of this species is round and small, but definite. The margin of the pileus is even and does not exceed the gills. The surface is granular especially on the umbo and growing less dense toward the margin. In older specimens the surface of the margin may not be granular. When young, the center of the pileus is uniformly ochraceous but later it becomes auburn shading through Sanford-brown to tawny, ochraceous tawny or even buff on the margin.

The universal veil covers the entire lower half of the stipe forming a definite membranous sheath whose upper end flares out and up into a broad conspicuous collar, the annulus. This sheath is just like a close fitting boot and can be peeled off of the stem with ease. It is the character of this persistent annulus which makes it fairly easy to distinguish this species.

It is not very common around Seattle and does not entirely agree with Kauffman's description of the species. It is similar to A. amianthina but is larger and the annulus is more pronounced. It has been collected on the Tacoma "prairies" and on San Juan Island.

5. Armillaria rugoso-reticulata (Lorin) Zeller, Mycologia 25: 378. 1933.

Syn.: Lepiota rugoso-reticulata Lorin, Oesterr. Bot. Zeits. 1879.

This species resembles A. granulosa in color but differs in its slender stem and rugose pileus. It approaches A. granosa in the character of the pileus but it is small and the annulus is rarely persistent. It differs from A. amianthina in the lack of an umbo and small spores. The spore measurements follow very closely those reported by Zeller,  $4-6 \times 3-3.5 \mu$ .

This species is rather rare. The specimens examined showed the rugose pileus very clearly, especially when young. The pileus measures up to 3 cm. broad; convex to campanulate becoming expanded and later plane sometimes with a small, shallow umbo. It exceeds the gills by about one mm. or less and is always conspicuously appendiculate with more or less triangular patches. The color when very young is Sudan brown, becoming near Buchthorn brown but darker, eventually becoming uniformly an antimony yellow.

6. Armillaria amianthina (Fries) Kauff. Papers Mich. Acad. Sci. 2: 60. 1922.

Syn.: Lepiota amianthina Fries, Monog. Hymen. Suec. 1: 29. 1857; Hymen. Eur. 27. 1874.

The surface of pileus of this species is characteristically granulose although it may vary in color. It is found very commonly on the San Juan Islands on coniferous logs, in moss, under vine maple, Douglas fir, hemlock, and spruce. The color variation apparently is due to the environment in which it grows. When growing in very moist places under trees the pigments are intense while in the open the pigments seem to be bleached out and the color is much lighter.

In the specimens collected, the pileus has not exceeded 4.5 cm. broad and is obtusely convex but not definitely umbonate. The margin at first somewhat exceeds the gills and tends to form triangular appendiculate flaps in some of the specimens, but it becomes incurved and wavy with age. The surface is densely granulose and sometimes finely, radially rugose on the margin extending

about half way to the center of the pileus. The young specimens have the center of the pileus a Buckthorn brown with the margin antimony yellow; in the older specimens the center is ochraceous tawny while the margin is ochraceous buff. The gills are squarely

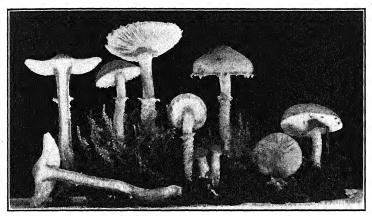


Fig. 1. Armillaria amianthina.

adnate, broad and pointed at the margin alternating long and short. The stem varies from 3–6 cm. long and 3–6 mm. thick. It is cylindrical, equal to slightly thickened toward the base, hollow, and fibrous. The surface is floccose-granular on the lower half and fibrous on the upper portion. It ranges from Buckthorn brown below to ochraceous buff above, becoming Sayal brown with age.

7. Armillaria granulosa (Fries) Kauff. Papers Mich. Acad. Sci. 2: 60. 1922.

Syn.: Lepiota granulosa Fries, Syst. Myc. 1: 24. 1821.

This species is not very common in the Pacific Northwest. It has been collected on San Juan Island among moss under Douglas fir trees. It resembles A. amianthina, A. granosa, and A. rugosoreticulata but is distinguished from all of them by the attachment of the gills which are adnexed. This seems to be the main distinguishing character of the species although the pileus is rather striking in color being ochraceous and tinted brick red.

8. Armillaria cinnabarina (Fries) Kauff. Papers Mich. Acad. Sci. 2: 60.

Syn.: Lepiota cinnabarina Fries, Monog. Hymen. Suec. 1: 29. 1857; Hymen. Eur. 36. 1874.

This species is extremely rare in the Pacific Northwest. It has been collected on Mt. Hood, Oregon, by Kauffman (15) and by the writer on San Juan Island and near Index, Washington.

There is a question as to whether this species should be included in this genus. The gills range from nearly free to distinctly adnexed but at times they are definitely free. This factor would eliminate it from this genus except that the specimens with the free gills are very much in the minority. I have found only one whose gill-attachment could be called free.

## 9. Armillaria granulosoides Zeller, Mycologia 25: 377. 1933.

This species was first reported by Zeller in Oregon in 1933 (25) and due to its resemblance to A. granulosa he named it A. granulosoides. It grows consistently in mossy places, sometimes in the open and sometimes along the edge of Douglas fir timber. The writer has collected it around Chase Lake and near Richmond Heights, Washington.

## 10. Armillaria badicephala Zeller, Mycologia 27: 459. 1935.

This species was reported first in Oregon by Zeller in 1935 (28). It has the general appearance of *Tricholoma*. Our specimens fit exactly the description given by Zeller. Found chiefly in coastal regions but also inland around lake and coniferous wood region. Collections were made by the writer in the vicinity of Chase Lake, Washington.

# 11. Armillaria viscidipes Peck, N. Y. State Mus. Bull. 44: 15. 1891.

In 1922, Kauffman found this species on Mt. Hood, Oregon (14, 15). He made a careful study of it as it occurs in the Pacific Northwest and suggests some modifications of Peck's original description. The spores are slightly smaller than the size given by Peck. The gills are adnate at first, becoming "slightly acummate-decurrent" and sinuate in old plants.

Armillaria ponderosa (Peck) Sacc. Syll. Fung. 5: 58. 1887.
 Syn.: Armillaria magnivelaris (Peck) Murr. N. Am. Flora 10: 37. 1914.

Armillaria arenicola Murr., Mycologia 4: 212. 1912.

This species is usually found in sandy soil, either in the open or under pine or Douglas fir. It has been collected near Port Angeles, on Bainbridge Island and on San Juan Island. Zeller (27) has

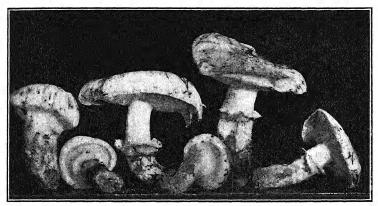


Fig. 2. Armillaria ponderosa.

described this species quite thoroughly and compared it with A. magnivelaris (Peck) Murr. and also with a closely related Japanese species A. matsutake Ito & Imai. See his article for further details (27).

## 13. Armillaria albolanaripes Atk. Ann. Myc. 6: 54. 1908.

This species has been collected in Oregon and Washington by Zeller (25) and also by Kauffman (14, 15). The writer has found it rather sparingly in the low lands of Snohomish County, Washington, under conifers in late November. The species may be recognized by the bright yellow or yellowish-brown color of the pileus which is darker at the center.

## 14. Armillaria aurantia Fries, Syst. Myc. 1821.

Syn.: Tricholoma aurantium Fries, Hymen. Eur. 41. 1874.

As has been mentioned, A. dryina and A. corticata resemble rather closely Pleurotus and A. granosa and A. granulosa seems

related to *Lepiota*, so in *A. aurantia* we find a species approaching very closely to *Tricholoma*. Kauffman, in his Agaricaceae of Michigan (13), describes it as an *Armillaria* while in a later article (15) he places it among the "Doubtful Species."

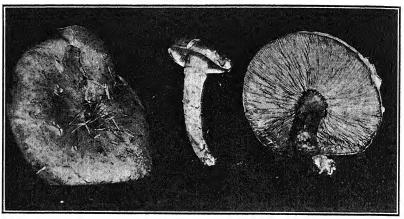


Fig. 3. Armillaria aurantia.

It is evidently on the borderline between the two genera. It has a veil but it seldom leaves an annulus. The gills are sinuate or emarginate and the structure of the trama is similar to *Tricholoma*. The gills, however, are adnexed although very slightly in some specimens. This adnexed condition of the gills is about the only excuse for placing it in the genus *Armillaria*, yet if we adhere strictly to the characteristic of the genus as already stated, that the gills of *Armillaria* may be "adnexed, adnate or decurrent," then it would seem that this is the proper place for it. There is room, however, for difference of opinion in regard to this species.

 Armillaria robusta Fries, Hymen. Eur. 41. 1874; Sacc. Syll. Fung. 5: 74. 1887.

Zeller (29) gives a detailed description of this species as it occurs in the Pacific Northwest. It grows under much the same conditions as A. ponderosa but is readily distinguished from it by the reddish or cinnamon color of the pileus and the orange spots on the disc. It is fairly common along the Coastal Regions of Washington during October and November (29).

36 3

The description in the key is adapted from Zeller's (25).

#### ACKNOWLEDGMENTS

I wish to thank Dr. J. W. Hotson for his kind assistance and suggestions in the preparation of this article, and Dr. D. E. Stuntz for his field notes and the use of his negative for figure 1.

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# STUDIES IN THE PATELLARIACEAE

ELLYS THEODORA BUTLER

(WITH 10 FIGURES)

#### INTRODUCTION

The task of monographing the North American species of the Patellariaceae was undertaken with the understanding that this family included a group of inoperculate Discomycetes, of the order Pezizales. Two interesting observations have greatly modified the course of this study. First, the discovery of a type of ascus dehiscence characteristic of certain Pyrenomycetes, but unknown in the Discomycetes, and secondly, the fact that many species placed in the Patellariaceae cannot be distinguished from species placed by lichenologists in the family Lecidiaceae of the Cyclocarpineae.

Historical Review: Fries established the genus Patellaria in 1822, placing it in his division Elvelaceae, suborder Cupulati. He divided the genus into two tribes, Subcoriaceae with four species, including P. atrata, and Subgelatinosae with three species, including P. pulla. The genus was characterized as follows: "Receptaculum marginatum, patellaeforme, semper apertum, epidermide contigua. Hymenium laeve, subpersistens; sed ex ascorum dissolutione pulverulentum. Asci connati absque paraphysibus. Cupula centro affixa, passim stipitata, libere evoluta (non erumpens), planiuscula. Velum nullum. Substantia lenta, subcoriacea, raro subgelatinose." In 1825 he placed the genus in a tribe of the same name, Patellarei, in the order Phacidiacei in the Pyrenomycetes. In 1849 (16) he made the Patellariaceae one of six orders in his new group the Discomycetes, and included the following genera: Cenangium, Heterosphaeria, Lachnella, Patellaria, Sphinctrina and Laquearia.

As more detailed studies of the Discomycetes progressed, a concept of the family Patellariaceae was gradually formed by mycologists based on these essential characters: apothecia superficial,

sessile, carbonaceous or coriaceous, black, glabrous, patelliform and marginate, or rarely elliptic; spores varying from one celled and hyaline to muriform and colored; paraphyses usually enlarged and colored above, forming a heavy epithecium. Included in the family were fungi growing as saprophytes on dead wood, and many that grow as parasites on lichen thalli.

Saccardo (39) at first included nine genera in the family and later (43) increased this number to thirty-three. His classification was based on spore septation. Rehm (35) divided the family into two groups, the Pseudopatellarieae with three genera, Patellea, Durella and Caldesia, characterized by a thin excipulum and narrow hypothecium, and the Eupatellarieae with seventeen genera including both saprophytes and lichen parasites distinguished by their thick excipulums and wide hypotheciums. He also included the Calicieae and Arthonieae as an "appendix" to this family, a classification not followed by any later workers. Lindau (24) followed Rehm's classification, including twenty-one genera, Boudier (4) included thirty genera, which were placed in his inoperculate group. Ramsbottom (34) treated twenty genera, and Clements and Shear (8) include thirty-five. Keissler (21) has described eleven genera of lichen parasites in this family.

Unfortunately, most of the species of this family are seldom collected, and many of them are known only from the original type specimens. Thus our knowledge of the group has been limited to the study of herbarium material and nothing is known of the complete life history or sexual stages of these fungi. Tulasne (48) figured pycnidial stages for Scutula epiblastematica and Abrothallus microspermus. Brefeld (5) reported the formation of conidia in cultures from ascospores of Patellea pseudosanguinea and of Patellea commutata, but his cultures of Biatorella resinae, Karschia lignyota and Patellaria proxima remained sterile. Lohman (26) cultured Hysteropatella Prostii and H. clavispora and found the pycnidial stages of the Hysterographium type.

Relationships: Although this family has been placed by mycologists in the order Pezizales, its close relationship to the lichens has long been recognized. Fries emphasized the great similarity between his genus Patellaria and the lichen genus Lecidea. Rehm pointed out that the Lecidiaceae may be distinguished from the

Patellariaceae only by the presence of algae. Lindau, recognizing this close relationship, noted that we often find lichens and fungi in the same genus. Schneider (45) believed that most of the lichen genera of the family Lecidiaceae were derived from different fungal ancestors in the Patellariaceae. A. L. Smith (46) says: "There is no doubt that the Cyclocarpineae derive from some simple forms of discomycetes in the Patellariaceae. The relationship between that family and the lower Lecideae is very close. A number of fungus genera in the Patellariaceae correspond to lichen genera in the Lecidiaceae." Clements and Shear believe that the main line of evolution of the lichens sprang from this family, and they further state (8): "It is practically certain that a considerable number of natural genera are artificially divided into lichen and non-lichen groups." They have placed several genera in both the Patellariaceae and in a lichen family. For example, Biatorella is also included in the Lecidiaceae, and Melaspilea in the Graphidaceae. Fink placed the Patellariaceae in the Pezizales saying that certain species of Patellea, Patinella, Karschia, Leciographa and Biatorella are lichens.

Recent investigations of the genera of the Patellariaceae formerly considered as fungi growing parasitically upon lichen hosts, have shown that they are provided with gonidia and may live as parasites, parasymbionts and finally as saprophytes on the underlying substratum (22, 44). These border-line genera have always been objects of controvery, the lichenologists treating them as true lichens, the mycologists as fungi in the Patellariaceae.

It is impossible to review here all the recent literature which has led most mycologists and lichenologists to the belief that lichens are fungi, and should be classified with the fungi. According to Fink's definition (14): "A lichen is a fungus which lives during all or part of its life in parasitic relation with an algal host and also sustains a relation with an organic or an inorganic substratum." The difficult problem of reclassifying the fungi to include the lichens, has so far been met only by interpolating large groups of lichens between the orders of fungi to which they seem most closely related. Fink (12) placed the lichens of the Cyclocarpineae in the order Lecanorales after the Pezizales, but said they cannot be more closely combined until more is known of the

complete life histories of many forms in both groups. Nannfeldt (30, p. 62) pointed out several distinguishing characters between the discolichens of the Lecanorales and the Pezizales. Aside from the difference in the habit of nutrition, the apothecia of the fungi in the Lecanorales are of longer duration than the Pezizales, the hyphae have a peculiar cartilaginous consistency, isolechenin is formed by most of them, the asci are thick walled, and the paraphyses form a heavy epithecium. He believed that many of the so-called "transition forms" in the Patellariaceae belong in the order Lecanorales.

This taxonomic study of the North American species of the Patellariaceae has revealed no characters by which many of the genera of the Patellariaceae can be separated from corresponding genera in the Lecidiaceae. I believe these genera should be combined. In structure of the apothecia, asci and spores, they show close relationship with the Phacidiaceae, Tryblidiaceae, and Hysteriaceae, as well as with the Lecidiaceae. The separation of many genera in these families has undoubtedly been artificial, but their true relationships can only be determined when sufficient comparative data of their complete life histories is available.

The discovery (6) of a type of dehiscence in Lecanidion atratum, that is typical of certain Pyrenomycetes, or the Ascoloculares according to Nannfeldt, has added one more complicating factor to the study of the natural affinities of this group. It has already been pointed out that the method of ascus dehiscence is considered a reliable criterion upon which to base large group relationships. It has not been possible so far to determine the method of ascus dehiscence for all the genera that have been included in the Patellariaceae. However, it is certain that some of them (for example Patellea, Durella and Patinella) do not have this type of dehiscence, and therefore should not be classified with Lecanidion atratum. It is extremely interesting that Nannfeldt, on the basis of different characters, had already separated these genera into other families in his order Helotiales. On the other hand, there are many genera which have been placed in other families, for example Tryblidiella in the Tryblidiaceae, which have the endoascus type of dehiscence and probably are more closely related with Lecanidion atratum. This type of dehiscence may form the basis for a new and more natural classification of the Patellariaceae, Phacidiaceae and Tryblidiaceae.

#### METHODS

These descriptions and drawings were made from dried herbarium material. The apothecia were softened with water, embedded in agar, and sectioned with a freezing microtome. For study of different stages of ascus development, crushed apothecia were mounted in lactophenol with added acid fuchsin and cotton blue (27). The iodine test was applied, but generally found unreliable in this material. Measurements of asci and spores were made from the longest and widest parts. Average measurements are given and strikingly different single exceptions are placed in parentheses. The "apex" of a spore is the end lying toward the apex of the ascus, as the spores are arranged within the ascus. Drawings were made with the aid of a camera lucida. The asci and spores of all the species in each genus were drawn at the same magnification, but a higher magnification was used for genera with small spores.

In the citation of herbarium specimens examined, the following abbreviations are used:

A = New York State Museum, Albany; B = Botanisches Museum der Universität, Berlin; B.M. = British Museum of Natural History, London; Br = Jardin Botanique de l'Etat, Brussels; E = Royal Botanic Garden, Edinburgh; F = Farlow Herbarium, Harvard University; G = Herbier Boissier and Institut de bontanique systematique de l'Université, Geneva; K = Royal Botanic Gardens, Kew; L = Persoon Herbarium, Leiden; N. Y. = New York Botanical Garden; P = Museum National d'Histoire Naturelle, Paris; St = Naturhistoriska Riksmuseum, Stockholm; U = Fries Herbarium, Uppsala; V = Naturhistorischen Museum, Vienna; W = Herbarium of the U. S. Dept. of Agr., Washington.

#### THE GENUS LECANIDION

Lecanidion Endl. Fl. Poson. 46. 1830.1

Patellaria Fries, Syst. Myc. 2: 158. 1822. Not Patellaria Hoffm. Pl. Lich. 1: 54. 1791.

Patella Chev. Fl. Envir. Paris 1: 302. 1826.

Cycledum Wallr. Fl. Crypt. Germ. 2: 511. 1833.

<sup>&</sup>lt;sup>1</sup> This genus is not to be confused with *Lecanidium* Massal., which according to Zahlbruckner is a synonym of *Pertusaria*.

Apothecia perennial and persistent, changing little upon drying. occurring scattered or gregarious upon dead wood or herbaceous stems, superficial, sessile, dark brown or black, carbonaceous, becoming soft when moist, orbicular, oblong or elliptic when young. typically patelliform and marginate when mature, the disk plane and smooth; the excipulum well developed, composed of parallel rows of hyphae, the outermost layers with thickened, dark colored walls; the wide hypothecium colorless, or colored somewhat lighter than the excipulum; asci cyindric or clavate, the wall thickened at the apex, 4-8 spored; the spores ejected forcefully from the tip of an endoascus, the ectoascus rolling back in the form of a wrinkled ring; spores 3 to many septate, spindle or club-shaped. often curved, typically biseriate, hyaline and filled with oil droplets, frequently germinating within the ascus; paraphyses numerous, branched, septate, with enlarged colored tips closely agglutinated forming a heavy epithecium 2 above the asci.

The history of the generic name *Patellaria* is a complicated one, and particularly confusing as the name has been referred to different plants by mycologists and lichenologists.

The name *Patellaria* was first used by Ehrhart in 1789 as a name for *Lichen upsaliensis* L. in a list of "nomia usalia." According to Barnhart (3), these were not generic names proposed by Ehrhart, but a list of single names to be used alone without generic names, and they are untenable. Hoffman (19) in 1791, crediting Ehrhart with suggesting the name, validly published the generic name *Patellaria* for a group of lichens including the scutelliform lichens of Linnaeus and the crustaceous lichens of Michelli. Thirty-six species were placed in the genus, about half of which Hoffman himself later divided into several genera.

Persoon (32) adopted the name Patellaria placing the genus in the family Scutellis and including two species, both of which Hoffman later placed in the genus Verrucaria. Acharius (2) used Patellaria as a tribe of crustaceous lichens. Five years later he (1) established the genus Lecidea and many of Hoffman's species of Patellaria were placed in the section Catillaria of the genus Lecidea. The remaining species of Patellaria were divided among several different genera and the name Patellaria was not retained

<sup>&</sup>lt;sup>2</sup> The term "epithecium" is used here as defined by Clements and Shear (8, p. 442), not in the sense of the lichenologists (14) for a structureless thalloid remnant lying upon the hymenium.

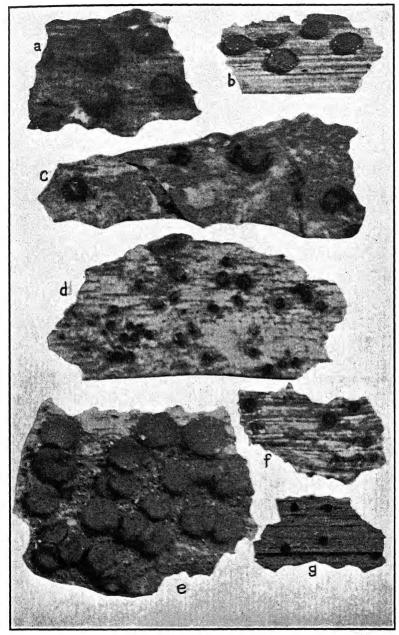


Fig. 1. Enlarged photographs of apothecia: a, Lecanidion simile; b, L. atratum; c, L. clavisporum; d, L. pusillum; e, Karschia stygia; f, K. lignyota; g, K. imperfecta.

for any of them. Since that time *Patellaria* has had a most fluctuating history as a lichen genus, having been completely dropped by many and retained usually in a still different sense by others.

DeCandolle (7) revived *Patellaria* Hoffm. in a modified sense. Leman (23) followed deCandolle, criticizing Acharius for not retaining the name for one of his sections—when he originally divided Hoffman's *Patellaria*. Müller Argeau (29) also used *Patellaria* in the sense of deCandolle. In 1890 Wainio (49) reduced *Patellaria* to synonymy and this course has been followed by all later lichenologists, including A. L. Smith and Zahlbruckner.

The greatest confusion came about when the name appeared in mycological literature for a genus of the cup-fungi, closely related to the lichens, established by Fries in 1822. In 1825 Fries (18) designated *Patellaria atrata*, with colorless septate spores, as the type of the genus *Patellaria* in the order Phacidiacei of the Pyrenomycetes. In 1828 he (15) divided the genus in two parts, the first typified by *P. atrata* he placed in the Pyrenomycetes, the second typified by *P. pulla* in the Tremellei.

According to the International Rules of Nomenclature, Patellaria Fries is not valid, as the name had been previously used. In 1830 Endlicher proposed the name Lecanidion for Patellaria Fries, including only the species L. atratum, so that it is clearly the type. Rabenhorst (33) followed Endlicher, making Patellaria Fries a synonym of Lecanidion. He is often erroneously credited with having proposed the name Lecanidion. Saccardo (39) accepted the name Lecanidion Endl., but retained the name "Patellaria Hedw. emend." in an entirely new sense for species with colored spores! Boudier (4) also used Patellaria Wahl. for species with colored septate spores. This is invalid. The name Patellaria can not be used for any of these fungi, and Patellaria Fries becomes a synonym of Lecanidion Endl.

#### KEY TO THE SPECIES OF LECANIDION

Asci with eight spores.

Apothecia with a black margin.

Paraphyses enlarged above.

Tips of paraphyses colored dark blue.

Tips of paraphyses bead-like and colored brown.

1. L. atratum.

2. L. clavisporum.

Paraphyses not enlarged above.

Apothecia with a prominent fuscous margin.

Asci with four spores.

L. pusillum.
 L. simile.

5. L. tetrasporum.

# 1. Lecanidion atratum (Hedw.) Endl. Fl. Poson. 46. 1830.

Lichen atratus Hedw. Descr. Musc. Frond. 2: 61. 1789.

Peziza patellaria Pers. Syn. Fung. 670. 1801.

Peziza atrata Wahlb. Flor. Ups. 465. 1820. Not Peziza atrata Pers. Syn. Fung. 669. 1801.

Patellaria atrata Fries, Syst. Myc. 2: 160. 1822.

Patella biformis Chev.3 Fl. Gen. Envir. Paris 1: 302. 1826.

Patellaria Verbasci Schw. Trans. Am. Phil. Soc. II. 4: 236. 1832.

Cycledum atrum Wallr. Fl. Crypt. Germ. 2:511. 1833.

Patellaria socialis De-Not. in Giorn. Bot. Ital. 2: 232. 1846.

Patellaria culmigena De-Not. in Giorn. Bot. Ital. 2: 232. 1846.

Opegrapha Lecanactis Massal. Symm. Lich. 64. 1855.

Ucographa atrata Massal. Symm. Lich. 64. 1855.

Patellaria concolor Fries, Hoffm. Ic. An. Fung. 99. 1865.

Pragmophora Lecanactis Koerb. Parerg. Lichen. 279. 1865.

Patellaria indigotica Cooke & Peck, Ann. Rep. N. Y. State Mus. 25: 98. 1873.

Patellaria cyanea Cooke, Jour. Linn. Soc. 17: 142. 1880.

Durella atrata Rehm, Ascom. Lojk. 18. 1882.

Durella atrella Rehm, Ascom. Lojk. 18. 1882.

Durella socialis Sacc. Syll. Fung. 8: 791. 1889.

Lecanidion concolor Sacc. Syll. Fung. 8:796. 1889.

Lecanidion indigoticum Sacc. Syll. Fung. 8: 797. 1889.

Lecanidion cyaneum Sacc. Syll. Fung. 8: 801. 1889.

Patellaria atrata f. indigotica Rehm, Ann. Myc. 4: 337. 1906.

Patellaria Henningsii Ranojevie, Ann. Myc. 8: 354. 1910.

Lecanidion Henningsii Sacc. & Trott. Syll. Fung. 22:756. 1913.

Apothecia scattered or usually thickly gregarious (FIG. 1b), at first slightly sunken and closed, globose or hysteriform, at maturity expanded, superficial, sessile, typically patelliform or occasionally elliptical, with an elevated margin, reaching a diameter of from

<sup>&</sup>lt;sup>3</sup> This is indexed as *Patellaria biformis*. Fries in Elench. Fung. 2: 15. 1828 cites *P. difformis* Chev. as a synonym of *Patellaria atrata*, a mistake in spelling copied later by others.

0.5–1.7 mm.; black, smooth, carbonaceous when dry, subgelatinous when moist, disc smooth, plane or slightly convex; excipulum 20-40 μ thick, composed of close parallel septate hyphae, the inner periclinal hyphae thick walled and hyaline, the outermost rows with thick brown-black walls; hypothecium 50–80  $\mu$  wide, the cells just below the hymenium with thin hyaline walls, those of the basal part elongated and with dark thickened walls (Fig. 2A): asci clavate (FIG. 4), short stipitate, rounded above with the wall thickened at the apex, reaching a length of from 70–157  $\mu$  and a diameter of 15–20  $\mu$  (average length 90–122  $\mu$ ), 8 spored; spores irregularly biseriate, clavate, with the apex blunt and gradually tapering below, often slightly curved, hyaline, 5-11 septate, the cells usually containing 1 or more oil drops, 20–50  $\mu$  long by 6–12  $\mu$ wide (average length  $30-45 \mu$ ). Paraphyses numerous, filiform. septate, branched above with the tips enlarged to  $4-6 \mu$  wide and colored dark blue, rarely olive-brown, extending above the asci and closely agglutinated forming a thick epithecium.

On a wide variety of woody and herbaceous stems, old rugs, old paper and sacking.

TYPE LOCALITY: Europe.

DISTRIBUTION: Throughout Europe, North America, Mexico, Bermuda and Hawaii.

Specimens examined: Anderson, Parasitic Fungi of Montana, 571 (N. Y.); Ansi, Lich. rar. Veneti 96 (K, N. Y., St, V); Ayer, on Salix (K); Baker, C. F., Pacific Slope Fungi 179 (B, P, N. Y., V); Bartholomew, Kansas Fungi 485 (N. Y.); 943 (N. Y.); 1046 (N. Y.); Flora of Kansas, March 20, 1896 (St); Berkeley, 80 (K); 336 (K); 3350 (K); Bethel, Colorado 330 (N. Y.); Bisby, 1649 (N. Y.); Bisby, Buller & Hanna, 4651 (N. Y.); Bisby & Gordon, 4650 (N. Y.); Blake, 130 (N. Y.); Bloxam, "Gallo Provincio" (B. M.); Boudier, Abbe Gretes (P); Brenckle, Fungi Dak. 586 (N. Y.); 665 (N. Y.); 698 (St); South Dakota Fungi 1766 (N. Y.); Brongniart, "Lichen atratus" (P); Brown, Britton & Seaver, Bermuda 19 (N. Y.); 22 (N. Y.); 1223 (N. Y.); 1466 (N. Y.); Caldesi, Erb. Critt. Ital. II. 821 (Br, G); Cavara, Fung. Longobard. 167 (B, B. M., N. Y., V, W); Cooke, 27 (Ed); 350 (K); Fungi Brit. Exs. 194 (Ed, K); Cummins, 98 (N. Y.); 98a (N. Y.); 99 (N. Y.); 100 (N. Y.); 144 (N. Y.); 172 (N. Y.); Dearness, 3413 (St); Desmazieres, Plantes Crypt. de France I. 429 (B. M., G, K, N. Y.); 41 (P); Earle, F. S., Flora of Alabama 151 (N. Y.); Earle, F. S. & Baker, C. F., Alabama Biol. Surv. 1/23 '97 (N. Y.); Earle, F. S. & Earle, Esther S., Plants of New Mexico, Lincoln Co. 7/26. 1900 (N. Y.); Earle, F. S. & Underwood, L. M., Flora of Alabama, Feb. 15, 1896 (N. Y.); Ellis, N. Am. Fungi 64 (A, Br, B. M., K, N. Y.); 893 (N. Y.); 1061 (N. Y.); 1258 (N. Y.); Ellis & Everhart, Fungi Columb. 746 (B. M., G, N. Y.); N. Am. Fungi 2051 (B. M., Br, F, K, N. Y.); Fairman, 14 (St); 1904 (A); Farlow, 395 (F, N. Y.); 1167 (B, N. Y.); Fautrey, Herb. Crypt. de la Cote D'Or 395 (P); Ferry, 531 (P); Fink, Ascomycetes of Ohio, col. by Bachman 7/31. 1907 (N. Y.); Flowtow, Lich. Exs. 257 (B); Fries, Lund (U); Fuckel, Enum. Fung. Nass. 765 (N. Y.); Fungi Rhenani 1118 (B. M., Br, F, G, K, N. Y., V); Gerard, N. Am. Fungi 1069 (B. M., N. Y.); Harkness, 2670 (B. M.); 2944 (B. M.); 2993 (B. M.); Holway, 352 (N. Y.); Johnson, 1563 (N. Y.); Kellerman & Swingle, 1414 (N. Y.); Koerber, Lich. Sel. Germ. 199 (G, N. Y., St); Kunze, Flora von Eisleben 533 (B); 1875 (St); Langlois, Flora Ludoviciana 271 (F, N. Y.); 1290 (N. Y.); 1638 (N. Y.); 2231 (N. Y.); Linabled, in Herb. E. Fries (U); Lowe, 172 (N. Y.); Morgan, 24 (N. Y.); 61 (N. Y.); 276 (N. Y.); 278 (N. Y.); 279 (N. Y.); 663 (N. Y.); 893 (N. Y.); Nees, Lugd. Bot. 910, 261-363 (L); Passerini, Erb. Critt. Ital. 1172 (G, V); Paris Herb., on Ribes, Torino (P) Type of P. socialis; Peck, 117 (N. Y.); Savannah (A, N. Y., K) Type of P. indigotica; Persoon Herb., Lugd. Bot. 910, 261-342 (L); 910, 261-360 (L); 910, 261-361 (L); 910, 256-838 (L); Petrak, Fl. Boh. & Mor. Exs. 272 (Br, E, N. Y.); Phillips, Elv. Brit. 90 (E, K, N. Y., W); Piskor, Flora Moravica IV. 1935 (N. Y.); Pringle, 1167 (N. Y.); Rabenhorst, Fungi Eur. 1612 (B, B. M., Br, G, K, N. Y., St, V); Ranojevic, 15.4. 1906 (St) Type of P. Henningsii; 302 (B); Ravenel, 223 (B. M., K, N. Y.) Type of P. cyanea; 518 (B. M.); 1445 (K, N. Y.); 1640 (B. M., K); Rehm, Ascomyceten 574 (B, Br, K, N. Y.); Lojka 51 (St); Lojka 194 (St); III. 1910 (St); Roumeguère, Fungi Gallici Exs. 828 (Br, G, K, N. Y.); Fungi Sel. Exs. 5526 (B, G, K, N. Y.); Saccardo, Myc. It. 1676 (N. Y., W); Myc. Ven. 263 (B. M., K, N. Y., St, V, W); 791 (P); Treviso (K, N. Y.); Schweinitz Herb. (K, N. Y., U) Type of P. Verbasci; Seaver, Iowa Fungi 108a (N. Y., St); 108b (N. Y.); Seaver & Bethel, Fungi of Colorado 1910 (N. Y.); Shear, Lincoln, Nebraska on Ulmus (W); 5903 (W); Smith, A. H. & Cummins, 100 (N. Y.); Sydow, Myc. Germ. 2719 (E, K); Myc. Mar. 4757 (B. M., N. Y.); Thaxter, R. 107 (N. Y.); Tulasne Herb., St. Cloud (P); Underwood, 52 (N. Y.); Waterston, 238 (N. Y.); Winter Herb., Fungi Hungarici-113 (St, V); Woronow, Fungi Caucasici 199 (St, N. Y.); Zwack, Lich. 444 (N. Y.).

This species was designated by Fries (18) as the type of the genus Patellaria. Specimens of Fries, Fung. Sclerom. Suec. no. 336 labeled Patellaria atrata, examined at Kew and Berlin do not conform to his description, and were named Tympanis confusa by Nylander (31). However, a specimen in the Fries Herbarium at Uppsala, collected in Lund, agrees in all respects with Fries' description of Patellaria atrata. This specimen is identical with four specimens in the Persoon Herbarium at Leiden, labeled Peziza Patellaria, and may be considered as authentic type material of this species. Fries (17) cites Peziza Patellaria Pers. as a synonym of Patellaria atrata. There are five other specimens in the Persoon Herbarium also labeled Peziza Patellaria which do not belong in the genus Lecanidion.

Patellaria indigotica Cooke & Peck was distinguished by the bluish tint of the hymenium, and as that color is also typical of Lecanidion atratum, and the type material agrees in all other respects with the latter, they are considered synonymous.

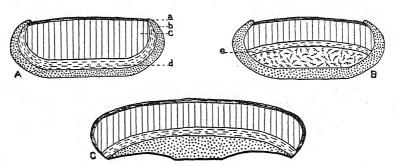


Fig. 2. Diagrams of sections through mature apothecia: A, Lecanidion atratum, a, epithecium, b, excipulum, c, hymenium, d, hypothecium; B, Lecanidion simile, e, region of hypothecium containing calcium oxalate crystals; C, Karschia stygia.

Patellaria cyanea Cooke was described as having spores 3–5 septate, but a study of type material showed that the spores may become 5–7 septate and it is identical with Lecanidion atratum.

A specimen of *Patellaria socialis* De-Not. apparently from the type collection, examined in the Paris Herbarium, agrees in all characters with *Lecanidion atratum*. The asci and spores are large, becoming 11 septate. This makes a wide range in ascus and spore size in *Lecanidion atratum*, but no other differences can be found for separating either the small spored or large spored types.

No material of *Patellaria concolor* Fries in Hoffm. has been available for study, but it is placed in synonymy here on the basis of Hoffman's description and illustration.

Specimens of *Patellaria Verbasci* Schw. from the Schweinitz Herbarium were examined at Kew, Uppsala, and The New York Botanical Garden. It is the same as *Lecanidion atratum*.

DeNotaris distributed material under the name *Patellaria cul*migena De-Not., and later wrote (10) that he considered it the same as *Patellaria atrata*. A specimen of *Patellaria culmigena* De-Not, examined in the Paris Herbarium is *Lecanidion atratum*. A specimen of *Patellaria Henningsii* Ran. on *Verbascum*, collected in Belgrade, apparently from the type collection, was examined in the Sydow Herbarium at Stockholm. It is identical with *Lecanidion atratum*.

The apothecia of this fungus are persistent, and were reported by Fries as perennial. It is not unusual to find germinating spores in the asci.

Lecanidion atratum has been described as a lichen with a thallus in the genera Plagmopara, Ucographa and Opegrapha. In the hundreds of specimens examined no thallus was found, although the apothecia occurring on wood are frequently closely associated with algae.

Currey (9) reported a second type of fructification; smaller plants without asci, the hymenium composed of a mass of clavate, septate spores, which he believed may be related to *Lecanidion atratum*. An asexual stage has not been more definitely reported for this species.

2. Lecanidion clavisporum (Berk. & Br.) Sacc. Syll. Fung. 18: 184. 1906.

Patellaria clavispora Berk. & Br. Ann. Mag. Nat. Hist. II. 13: 456. 1854. Not Patellaria clavispora (Peck) Sacc.

Patellaria Crataegi Phillips, Grevillea 17: 46. 1888.

Durella clavispora Sacc. Syll. Fung. 8: 794. 1889.

Lecanidion Crataegi Sacc. Syll. Fung. 8: 799. 1889.

Patellaria corticola Starb. Bih. K. Svensk. Vet. Akad. Handb. 21<sup>3</sup>: 23. 1895.

Lecanidion corticolum Sacc. & Sydow, Syll. Fung. 14: 821. 1899.

Apothecia erumpent or superficial from the beginning (FIG. 1c), sessile, subglobose at first, expanding at maturity, patelliform or somewhat irregular in shape, reaching a diameter of 0.5–2 mm., marginate, black, carbonaceous when dry, soft when moist and brown in color, white within, disc plane or slightly concave; excipulum about 80  $\mu$  thick, composed of closely interwoven hyphae with the walls thickened and dark brown, and arranged in parallel rows at the surface; hypothecium hyaline, brownish beneath gradually grading into the excipulum; asci cylindric-clavate with the wall slightly thickened at the rounded apex and staining blue with

iodine (FIG. 6), gradually tapering beneath to a slender stipe, reaching a length of from 90–160  $\mu$  and a diameter of 8–13  $\mu$ , 8 spored; spores biseriate above, uniseriate below, narrowly clavatefusiform with the apex rounded and tapering below to the acute base, straight or slightly curved, hyaline, 3–5 (6) septate, 21–36 (60)  $\mu$  long and 5–6  $\mu$  wide; paraphyses numerous, slender, septate, branched, enlarged above and colored brown with the irregularly nodulose tips (moniliform) closely adhering, forming a brown epithecium.

On Crataegus, Fagus grandifolia, Ligustrum and Quercus.

Type locality: Lucknam, Wiltshire, England.

DISTRIBUTION: Canada, England, Sweden, Switzerland.

Specimens examined: Berkeley, on Privet, Lucknam, Nov. 4, 1852 (K) Type of P. clavispora; Bloxam, 86 (K); Cooke, Capron (E); Oct. 1856 (K); Ann 774 (K); Cliff House (K); Currey, Bentham Hill, Oct. 1856 (K); Sept. 1862 (K); Eliasson, 27 (St, N. Y.) Type of P. corticola; Jackson, Crypt. Herb. Univ. Toronto 2861 (N. Y.); Massee, Twycross (N. Y.); Phillips, 3 Corbie Den 1/2/87 (B. M.) Type of P. Crataegi; Romell, 1/7.1887 (K, N. Y.).

There has been a great deal of confusion in this country as to the correct identification of Lecanidion clavisporum. This was due to the wide distribution in the Ellis and Morgan collections of specimens of Lecanidion atratum with asci and spores somewhat smaller than the average, incorrectly labeled Patellaria clavispora. This misidentification was the basis of Morgan's statement (28): "This species (P. clavispora) is commonly confused with P. atrata" and led to the general belief here that Patellaria clavispora is a synonym of Lecanidion atratum. The type specimen of Lecanidion clavisporum was studied in the Berkeley Herbarium at Kew and found to be a distinct species. It may easily be distinguished from Lecanidion atratum and L. simile by its brown moniliform paraphyses aptly described by Berkeley and Broome as follows: "Paraphyses branched, bearing at their tips one or more dark bodies sometimes arranged like the joints of a necklace." The paraphyses are so striking in structure that Currey (9, p. 227) believed they bore conidia, describing them thus: "The brown colour is entirely owing to the small brown stylospores or conidia which are attached to the tips of the paraphyses and which bear some resemblance to the spores of a Cladosporium."

The type specimen of Patellaria Crataegi Phillips was examined in the Phillips Herbarium at the British Museum and, although the asci and spores were somewhat larger than is typical for Lecanidion clavisporum, this was not considered of sufficient importance to keep the two species separate. An examination of material from the type collection (Eliasson no. 27) of Patellaria corticola in Rehm's Herbarium at Stockholm, and at The New York Botanical Garden, showed it to be identical with Lecanidion clavisporum.

It is unfortunate that fresh material of this species has not been available for study. Nannfeldt (30) considered it unrelated to Lecanidion atratum, but was uncertain where to place it. It is retained here, in the genus Lecanidion, until the type of ascus dehiscence is known and sufficient comparative data regarding the complete life history of these forms is available, so that its natural affinities may be determined.

3. LECANIDION PUSILLUM (Peck) Sacc. Syll. Fung. 8: 799. 1889. Patellaria pusilla Peck, Bull. N. Y. State Mus. Nat. Hist. 1<sup>2</sup>: 22. 1887.

Apothecia globose at first, later expanding and becoming patelliform with a narrow regular margin (Fig. 1d), reaching a diameter of from 0.5–0.8 mm., black, carbonaceous when dry, gelatinous when moist with the disc appearing a dirty gray, disc smooth, plane or slightly convex when moist; excipulum 22–39  $\mu$  thick composed of parallel rows of elongated cells with slightly thickened light brown walls; hypothecium about 66  $\mu$  wide colored a light brown; asci clavate (Fig. 5), gradually tapering below, rounded above with the wall slightly thickened at the apex, reaching a length of 59–82  $\mu$  and a diameter of 8–12  $\mu$ , not staining blue with iodine; spores irregularly crowded or biseriate, lanceolate or subclavate, 5–7 septate, 12–17  $\mu$  long by 2–4  $\mu$  wide; paraphyses numerous, filiform, not enlarged above.

On beech wood.

Type locality: Catskill Mountains, New York.

DISTRIBUTION: This species is apparently known only from the type collection in New York State.

Specimens examined: *Peck, 18* Catskill Mountains, N. Y. (A, N. Y.) Type.

The ascospores in this species give rise to hundreds of small spores, as in the genus *Tympanis*. This character is considered by most mycologists as a difference of generic significance. It is not possible, on the basis of the scanty herbarium material available for study, to ascertain any more closely the natural relationships of *Lecanidion pusillum*, and the species is retained here for the present.

4. Lecanidion simile (Gerard) E. T. Butler, comb. nov.

Patellaria similis Gerard, Bull. Torrey Club 5: 26. 1874.

Patellaria atrofusca Berk. & Curt. Grevillea 4: 2. 1875.

Cenangium concinnum Berk. & Curt. Grevillea 4: 5. 1875.

Patellaria oleosa Cooke, Bull. Buffalo Soc. Nat. Sci. 3: 26. 1877.

Patellaria fusco-atra Rehm in Ellis, N. Am. Fungi 447. 1880.

Lecanidion fuscoatrum Rehm; Sacc. Michelia 2: 141. 1880.

Durella fuscoatra Rehm, Ber. Nat. Ver. Augsburg 26: 113. 1881.

Scleroderris concinna Sacc. Syll. Fung. 8: 595. 1889. Durella similis Sacc. Syll. Fung. 8: 794. 1889. Lecanidion atrofuscum Sacc. Syll. Fung. 8: 800. 1889.

Apothecia superficial, sessile (FIG. 1a), at first orbicular with a prominent fuscous margin, later expanding and becoming patelliform, margin persistent, reaching a diameter of 0.5-1 mm., carbonaceous and shiny when dry, becoming gelatinous when moist, disc smooth, black, brown when moist, plane or slightly convex, chalky white within; excipulum 35–52  $\mu$  thick, composed of parallel rows of closely interwoven hyphae with thickened brown walls; hypothecium thick,  $208-230 \mu$  wide, the region just below the hymenium (26-39  $\mu$  wide) composed of hyphae colored a bright orange yellow, below that a hyaline region (182-195  $\mu$  wide) where the hyphae are completely covered by calcium oxalate crystals which give the characteristic chalky white appearance to the broken apothecia (FIG. 2B); asci cylindric-clavate (FIG. 7), short stipitate, the wall thickened and staining deep blue with iodine at the rounded apex, reaching a length of  $59.5-132 \mu$  and a diameter of  $10-14 \mu$ , 8 spored; spores irregularly crowded or biseriate above, uniseriate below, or rarely uniscriate throughout, fusiform-elliptical, straight or slightly curved, triseptate or rarely four-septate, hyaline, 14–22  $\mu$ long by  $3-4 \mu$  wide; paraphyses numerous, filiform, septate, branched and slightly wider above, encrusted with a brown substance, extending above the asci and closely agglutinated forming a heavy brown epithecium.

On Carya, Cercis, Laurus, Ligustrum, Quercus and Vitis.

Type locality: Poughkeepsie, New York.

DISTRIBUTION: Alabama, Delaware, Mississippi, Missouri, New Jersey, South Carolina, Virginia.

Specimens examined: Berkeley, 2460 (K, N. Y.); Commons, 2126 (N. Y.); Demetrio, 49 (N. Y.); Earle & Baker, 2256 (N. Y.); Alabama Biol. Surv. on Vitis rotundifolia 3/21. 1897 (N. Y.); Ellis, N. Am. Fungi 447 (B, B. M., K, N. Y.); 106a (N. Y.); Ellis & Everhart, Fungi Columb. 1226 (B. M., G, N. Y.); Gerard, on Quercus rubra, Poughkeepsie (K, N. Y.) Type of P. similis; Morgan, 1226 (N. Y.); Peters, 5238 (K) Cotype of C. concinnum; Ravenel, Fung. Am. Exs. 313 (B. M., K, N. Y.); 1678 (B, M., K, N. Y.) Type of P. oleosa; 2210 (F, K) Type of P. atrofusca; 2295, 3828, 6172 (K) Cotypes of C. concinnum; 2358 (B. M., K, N. Y.); Rehm, Ascomyceten 464 (B, B. M., F, K, N. Y., St) Type of L. fuscoatrum.

The apothecia of this species may be readily distinguished by the fuscous color beneath which extends up into the margin, and in cross section by the wide hypothecium containing calcium oxalate crystals, as well as by the asci and spores. The broken bases of old apothecia, having a characteristic chalky appearance are frequently persistent.

The number of the type species of *Patellaria atrofusca* Berk. & Curt. is mistakenly printed in the original description as Car. Inf. 3210. The number is 2210 on the type specimen which was examined in the Berkeley Herbarium at Kew and found to be identical with *Patellaria similis* Gerard. None of the material examined showed the character, "springing from a black thin stratum which surrounds the twigs" as described by Berkeley and Curtis.

Abundant type material of Patellaria fuscoatra Rehm (Ascom. 464) from Newfield, N. J., has been available for study and agrees in all respects with the type specimen of Gerard's species. The four cotypes of Cenangium concinnum and the type (Ravenel 1678) of Patellaria oleosa were examined at Kew and found to be identical with Patellaria similis. It is interesting to note that a specimen of Ravenel 1678 in the Ellis Collection at The New York Botanical Garden is labeled Patellaria fuscoatra in Ellis' handwriting, and Saccardo (40) cites this number as L. fuscoatrum.

Patellaria purpurea Petch is very similar to this species in ex-

ternal appearance, and the tip of the ascus stains blue, but it may be distinguished by its larger, long stipitate asci (reaching a length of  $160 \,\mu$ ), and larger, uniseriate spores.

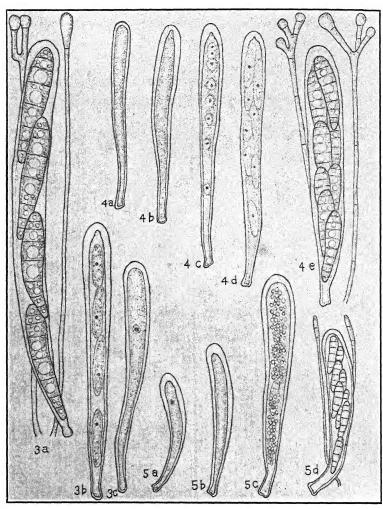


Fig. 3a. Paraphyses and mature ascus with spores of Lecanidion tetrasporum; b, c, younger stages in the development of the ascus. Fig. 4a-d. Development of the ascus of L. atratum; e, paraphyses and mature ascus with spores of L. atratum. Fig. 5a, b. Development of the ascus of L. pusillum; c, older ascus containing many small spores; d, paraphyses and mature ascus with spores.

5. Lecanidion tetrasporum (Massee & Morgan) Seaver, Proc. Iowa Acad. Sci. 12: 118. 1905.

Patellaria tetraspora Massee & Morgan, Jour. Myc. 8: 180. 1902.

Apothecia usually gregarious, occasionally scattered, superficial, ellipsoid at first with the margin vertically striate, expanding and at maturity reaching a diameter of 0.5-1 mm., patelliform with a persistent margin, black, smooth, carbonaceous, and somewhat gelatinous when moist, disc smooth and plane; excipulum and hypothecium similar to Lecanidion atratum; asci cylindric (FIG. 3), abruptly narrowed below into a short and slender stipe, rounded above with the wall slightly thickened at the apex, varying in length from  $125-190 \mu$  and in diameter from  $12-14 \mu$  (average length  $140-160 \mu$ ), 4 spored; spores uniseriate, clavate, with the apex blunt and the base acute, 6-9 septate, the cells containing 1 or more large conspicuous oil drops, 38–70 μ long by 10–11 μ wide (average length  $40-50 \mu$ ); paraphyses numerous, slender, septate and branched above with the thickened tips colored a deep blue and closely agglutinated forming a heavy blue epithecium above the asci.

On Acer saccharinum, Aralia spinosa, Juglans cinerea, Ulmus. Type Locality: Preston, Ohio.

DISTRIBUTION: Alabama, Connecticut, Iowa, Louisiana, Massachusetts, Michigan, New York, Ohio, West Virginia, Wisconsin and Canada.

Specimens examined: Baker, 395 (N. Y.); Berkeley Herb., 936 (K); Cook, O. F., 140 (N. Y.); Cunmins, 101 (N. Y.); 103 (N. Y.); Curtis, 1378 (P); Dearness, 1088 (N. Y.); Earle & Baker, Alabama Biol. Surv. on old stump 1/23/97 (N. Y.); Ellis, 1004 (N. Y.); Fairman, Lyndonville, N. Y. Oct. 188— (N. Y.); Farlow Herb., Lincoln, Mass. on oak, April 2, 1899 (F); Langlois, 271 (N. Y.); Massee & Morgan, 31 (N. Y.); Morgan, 25 (N. Y.) Type; 60 (N. Y.); 264 (N. Y.); Nuttal, Flora of Fayette Co., W. Va. 359 (N. Y.); Seaver, Iowa Fungi, Nov. 6, 1905 (N. Y.).

This species was formerly reported only from Iowa and Ohio. In going through collections of North American Patellariaceae, numerous specimens of *L. tetrasporum* were found incorrectly identified as *P. atrata* or *P. indigotica*. This was probably due to their close resemblance in external appearance and the similar bluish color of the paraphyses. *L. tetrasporum* is distinguished from *L. atratum* by the narrower cylindric asci which contain four

uniseriate spores. As the four spored condition is constant, apothecia never having both 8 spored and 4 spored asci, it is retained as a distinct species.

The statement by Massee & Morgan (28) that Patellaria tetraspora is allied to Patellaria clavispora Berk. & Br. is undoubtedly accounted for by Morgan's misconception of the true identity of P. clavispora. (See the discussion under L. clavisporum.)

## DOUBTFUL AND EXCLUDED SPECIES

THE DWING OUT I

Patellaria abictina Cooke, Grevillea 7: 4. 1878. = Patinella abictina (Cooke) Sacc. Syll. Fung. 8: 771. 1889.

Patellaria acericola Atk. in herb. Albany. (Lecanidion acericolum Atk. in Peck, Ann. Rep. N. Y. State Bot. 49: 24. 1896. — Dermatea acerina (Peck) Rehm, Ber. Bayer. Bot. Ges. 13: 197. 1912.

Patellaria agyrioides Rehm, Hedwigia 39: 322. 1900. No material of this species has been seen but according to von Höhnel, Sitzb. K. Akad. Wiss. Wien, Math. Nat. Kl. Abt. 1, 127: 558. 1918, it belongs in the genus Melittosporium Corda.

Patellaria applanata Berk. & Curt. Jour. Linn. Soc. 14: 108. 1875. = Catinella nigroolivacca (Schw.) Durand, Bull. Torrey Club 49: 16. 1922.

Patellaria atrovinosa Blox. in Berk. & Br. Ann. Mag. Nat. Hist. III. 15: 447. 1865. = Durella atrovinosa (Blox.) Sacc. Syll. Fung. 8: 794. 1889.

Patellaria aureococcinea Berk. & Curt. in Ellis, N. Am. Fungi I. no. 63. 1878. = Solenopezisa aureococcinea (Berk. & Curt.) Rehm, Ann. Myc. 2: 352. 1904.

Patellaria californica Rehm, Ann. Myc. 9: 367. 1911. No material of this species has been available for study.

Patellaria carolinensis Ellis & Ev. Jour. Myc. 1: 152. 1885. = Scutularia carolinensis (Ellis & Ev.) Sacc. Syll. Fung. 8: 808. 1889.

Patellaria carpinea (Pers.) Berk in herb. Berk, at Kew. = Pezicula carpinea (Pers.) Tul. Sel. Fung. Carp. 3: 183. 1865.

Pateilaria cenangicola Ellis & Ev. Jour. Myc. 4: 56. 1888. = Godroniopsis quernea (Schw.) Diehl & Cash, Mycologia 21: 244. 1929.

Patellaria clavata Ellis, Bull. Torrey Club 8: 74. 1881. = Belonidium clavatum (Ellis) Rehm, Ann. Myc. 2: 354. 1904.

Patellaria clavispora (Peck) Sacc. Syll. Fung. 8: 787. 1889. = Hysteropatella clavispora Seaver, Bull. Lab. Nat. Hist. State Univ. Iowa 6: 113. 1910. This is a homonym and must be renamed.

Patellaria congregata Berk. & Curt. in Massee, Jour. Linn. Soc. 35: 109. 1901. = Durella compressa Tul. Sel. Fung. Carp. 3: 177. 1865.

Patellaria connivens Fries, Summa Veg. Scand. 366. 1845. = Durella connivens Rehm, Ber. Nat. Ver. Augsb. 26: 9. 1881.

Patellaria constipata Berk. in Cooke, Handb. Brit. Fung. 720. 1871. = Pezicula livida (Berk. & Br.) Boud. Disc. Eur. 159. 1907.

Patellaria Cucurbitaria Rehm, Ascom. 311. 1875. = Blitrydium Cucurbitaria (Cooke) Sacc. Syll. Fung. 8: 804. 1889.

- Patellaria cyanea Ellis & Martin, Jour. Myc. 1: 97. 1885. = Patellea cyanea Sacc. Syll. Fung. 8: 784. 1889. This is a homonym and must be renamed.
- Patellaria cylindrospora Ellis, Bull. Torrey Club 6: 108. 1876. = Scutularia cylindrospora Sacc. Syll. Fung. 8: 808. 1889.
- Patellaria difformis Lambotte, Flore Myc. Belg. 275. 1880. = Biatorella difformis (Fries) Rehm in Rab. Krypt.-Fl. 3: 306. 1895.
- Patellaria dispersa Gerard, Bull. Torrey Club 5: 26. 1874. This species belongs in the genus Blitrydium.
- Patellaria fenestrata Cooke & Peck, Ann. Rep. N. Y. State Mus. 28: 68. 1879. = Blitrydium fenestratum Sacc. Syll. Fung. 8: 805. 1889.
- Patellaria ferruginea Cooke & Ellis, Grevillea 5: 91. 1877 [as fuliginea Sacc. Syll. Fung. 8: 787. 1889]. = Dermatea ferruginea Rehm, Ann. Myc. 2: 353. 1904.
- Patellaria flexella (Ach.) Phill. Brit. Disc. 362. 1887. = Lithographa flexella (Ach.) Zahlb. in E. & P. Nat. Pfl. 11: 93. 1903.
- Patellaria gnaphaliana Cooke & Ellis, Grevillea 6: 92. 1878. = Pyrenopeziza gnaphaliana Rehm, Ann. Myc. 2: 354. 1904.
- Patellaria Hamamelidis Peck, Ann. Rep. N. Y. State Mus. 33: 32. 1880.

   Dermatella Hamamelidis Durand, Bull. Torrey Club 29: 464. 1902.
- Patellaria hirneola Berk. & Br. Jour. Linn. Soc. 14: 108. 1875. = Catinella nigroolivacea (Schw.) Durand, Bull. Torrey Club 49: 16. 1922.
- Patellaria Hyperici Phill. Grevillea 10: 69. 1881. = Durella atrocyanea Höhnel, Ann. Myc. 16: 210. 1918.
- Patellaria inclusa (Pers.) Karst. Myc. Fenn. 1: 236. 1871. = Odontotrema inclusum Karst. Rev. 146. 1885.
- Patellaria Lecideola Fries, Summa Veg. Scand. 366. 1845. = Durella Lecideola Rehm, Ascom. Lojk. 19. 1882.
- Patellaria leptosperma Peck, Ann. Rep. N. Y. State Mus. 30: 62. 1878. = Holwaya gigantea (Peck) Durand, Bull. Torrey Club 28: 354. 1901.
- Patellaria leucochaetes Ellis & Ev. Jour. Myc. 1: 152. 1885. = Scutularia leucochaetes Sacc. Syll. Fung. 8: 809. 1889.
- Patellaria livida Berk. & Br. Ann. Mag. Nat. Hist. 13<sup>2</sup>: 466. 1854. = Pesicula livida (Berk. & Br.) Boud. Disc. Eur. 159. 1907.
- Patellaria Lonicerae Phill. Brit. Disc. 364. 1887. = Durella vilis Starb. Bih. Svensk Vet. Akad. Handb. 213: 22. 1895.
- Patellaria lurida Berk. & Curt. in Phill. Grevillea 19: 75. 1891. = Phacidium luridum (Berk. & Curt.) Phill. Grevillea 19: 75. 1891.
- Patellaria melaleuca Fries, Summa Veg. Scand. 366. 1845. = Mollisia melaleuca Sacc. Syll. Fung. 8: 337. 1889.
- Patellaria melaxantha Fries, Summa Veg. Scand. 366. 1845. = Blitrydium melaxanthum Sacc. Syll. Fung. 8: 806. 1889.
- Patellaria minor Karst. Myc. Fenn. 1: 233. 1871. = Odontotrema minus Nyl. Lich. Scand. 249. 1861.
- Patellaria nigrocinnabarina Schw. Trans. Am. Phil. Soc. II. 4: 236. 1832.

  = Rhytidopexisa nigrocinnabarina Sacc. Syll. Fung. 10: 65. 1892.
- Patellaria nigrocyanea Phill. & Hark. Bull. Calif. Acad. Sci. 1: 24. 1884. = Durella nigrocyanea Sacc. Syll. Fung. 8: 793. 1889.
- Patellaria nigroolivacea Fries in Cooke, Bull. Buffalo Soc. Nat. Sci. 3: 26.

1877. = Catinella nigroolivacea (Schw.) Durand, Bull. Torrey Club 49: 16. 1922.

Patellaria nigrovirens Sacc. & Ellis, Michelia 2: 572. 1880. This species belongs in the genus Leciographa.

Patellaria olivacea (Batsch) Phill. Brit. Discom. 361. 1887. = Catinella nigroolivacea (Schw.) Durand, Bull. Torrey Club 49: 16. 1922.

Patellaria olivaceovirens (Schw.) Fries, Syst. Myc. 2: 159. 1822. A fragmentary specimen of this species examined at Kew was a lichen.

Patellaria Peckii House, Bull. N. Y. State Mus. 22: 233. 1921. = Hystero-patella clavispora Seaver, Bull. Lab. Nat. Hist. State Univ. Iowa 6: 113. 1910.

Patellaria proxima Berk. & Br. Ann. Mag. Nat. Hist. 73: 450. 1861.=

Durella atrocyanea (Fries) Höhnel, Ann. Myc. 16: 211. 1918.

Patellaria pulla nigroolivacea Fries, Syst. Myc. 2: 160. 1822. = Catinella nigroolivacea (Schw.) Durand, Bull. Torrey Club 49: 16. 1922.

Patellaria Ravenelii (Berk. & Curt.) Cooke, Bull. Buffalo Soc. Nat. Sci. 3: 26. 1877. The specimens examined were sterile.

Patellaria recisa Berk. & Curt. in Cooke, Bull. Buffalo Soc. Nat. Sci. 3: 27. 1877. = Gorgoniceps Guernisaci Sacc. Syll. Fung. 8: 505. 1889.

Patellaria rhabarbarina Berk. Grevillea 4: 2. 1875. = Pezicula rhabarbarina (Berk.) Tul. Sel. Fung. Carp. 3: 183. 1865.

Patellaria Rhododendri Schw. Trans. Am. Phil. Soc. II. 4: 236. 1832. No material has been available for study.

Patellaria Rubi Libert, Pl. Ard. 231. 1834. = Pesicula rhabarbarina (Berk.)
 Tul. Sel. Fung. Carp. 3: 183. 1865.

Patellaria signata Ellis & Ev. Bull. Washington Lab. Nat. Hist. 1: 4. 1884.

= Blitrydium signatum Sacc. Syll. Fung. 8: 807. 1889.

Patellaria sphaerospora Berk. & Curt. in Cooke, Bull. Buffalo Soc. Nat. Sci. 3: 26. 1877. = Lagerheima sphaerospora Sacc. Syll. Fung. 10: 55. 1892.

Patellaria subsidua Cooke & Ellis, Grevillea 6: 8. 1878. = Blitrydium subsiduum Sacc. Syll. Fung. 8: 805. 1889.

Patellaria subtecta Cooke in Phill. Brit. Discom. 365. 1887. = Durella atrocyanea (Fries) Höhnel, Ann. Myc. 16: 211. 1918.

Patellaria subvelata Ellis & Ev. Jour. Myc. 1: 152. 1885. This is a species of Arthonia.

Patellaria triseptata (Karst.) Sacc. Syll. Fung. 8: 787. 1889. = Leciographa triseptata Morgan, Jour. Myc. 8: 180. 1902.

Patellaria tuberculosa Ellis, Bull. Torrey Club 8: 74. 1881. = Belonidium clavatum (Ellis) Rehm, Ann. Myc. 2: 354. 1904. The types of P. tuberculosa and B. clavatum were examined in the Ellis Collection at The New York Botanical Garden. Both species occur on old stems and leaves of Andropogon, and are identical.

Patellaria violacea Berk. & Br. Jour. Linn. Soc. 14: 108. 1875. = Catinella nigroolivacea (Schw.) Durand, Bull. Torrey Club 49: 16. 1922.

Patellaria viticola Pers. Myc. Eur. 1: 309. 1822. No specimens were available for study.

### THE GENUS KARSCHIA

KARSCHIA Koerb. Parerg. Lich. 459. 1865.

Poetschia Koerb. Parerg. Lich. 280. 1861.

Karschiella Sacc. Syll. Fung. 18: 177. 1908.

Epilichen Clements, Gen. Fung. 69. 1909.

Buelliella Fink, Lich. Fl. U. S. 372. 1935.

Apothecia scattered on dead wood or lichen thalli, superficial, globose when young, becoming patelliform at maturity and usually immarginate, disc flat or convex when moist, black, coriaceous or carbonaceous, softening when moist; excipulum pseudoparenchymatous composed of dark walled spherical or hexagonal cells; hypothecium thick and usually colored; asci clavate, with the wall thickened at the rounded apex, 8 spored; spores clavate, oblong or elliptic, two-celled, usually with one or more oil drops in each cell, becoming brown; paraphyses septate, branched, colored at the tips and closely agglutinated with extraneous material forming a heavy colored epithecium.

Karschia is one of the most interesting genera on that confusing border line between the lichens and the fungi. It has been placed in the Patellariaceae by most workers, but was considered by Nannfeldt (30, p. 65) as a group reduced from the Physiaceae.

The fungi placed in this genus grow either as saprophytes on wood or as parasites on other lichens. Saccardo suggested the subgenus Karschiella for those forms parasitic on lichens, and Clements made a new genus, Epilichen, for the parasitic species. Fungi with apothecia agreeing in structure with Karschia, but with a definite or evanescent thallus, are placed in the lichen genus Buellia. Fink proposed the new genus Buelliella for the species of Buellia that grow as parasites on other lichens. There are no morphological characters for separating these genera. This raises the difficult question of basing generic divisions entirely on physiological differences. A number of species are known as "facultative lichens," for they may live part of the time without gonidia, as saprophytic fungi. Reinke (38) has reported this condition for Buellia myriocarpa. Tobler (47) says that Karschia destructans grows as a parasymbiont on the thallus of Chaenotheca chyrsocephala, penetrates through the thallus living as a parasite on the algae and finally lives as a saprophyte on the bark beneath. When a single plant has these varied methods of nutrition in its life cycle, one immediately sees the fallacy of separating genera on that distinction alone. For in this case one would be faced with the ridiculous situation of calling the fungus Epilichen at first, then Buellia, and finally Karschia. I believe that these genera should all be combined. Buellia is the oldest name and by the rule of priority will be used for the group. According to Fink (12) Buellia belongs in the Lecidiaceae in his order Lecanorales. A. L. Smith (46, p. 341) and Zahlbruckner make a separate family for Buellia and Rinodina, the Buelliaceae, closely allied to the Physiaceae. Only the North American species of Karschia are discussed here. A study of the genus Buellia has been started, and the genera will be combined as quickly as possible.

### KEY TO THE SPECIES OF KARSCHIA

Apothecia attached by a central point.

Excipulum composed of large hexagonal cells. 1. K. stygia.

Apothecia not attached by a central point.

Hymenium yellow-green in section.

Spores "slipper shape."

Hymenium colorless in section.

Spores elliptic-cylindric.

2. K. lignyota.

3. K. imperfecta.

1. Karschia stygia (Berk. & Curt.) Massee, Jour. Linn. Soc. **35**: 107. 1901.

Patellaria stygia Berk. & Curt. Grevillea 4: 2. 1875.

Patellaria nigerrima Sacc. Atti Soc. Veneto Sci. Nat. Padova IV. 1: 29. 1875.

Patellaria fusispora Cooke & Peck, Ann. Rep. N. Y. State Mus. 28:67. 1876.

Patellaria Bloxami Berk. in Phill. Brit. Disc. 361. 1887.

Karschia fusispora Sacc. Syll. Fung. 8: 781. 1889.

Patellea stygia Sacc. Syll. Fung. 8: 783. 1889.

Karschia Bloxami Sacc. Syll. Fung. 8: 781.

Karschia nigerrima Sacc. Syll. Fung. 8: 780. 1889.

Karschia Taveliana Rehm in Rab. Krypt.-Fl. 1<sup>3</sup>: 1223. 1896.

? Karschia elaeospora Fairman, Proc. Rochester Acad. Sci. 6: 105. 1921.

Apothecia scattered or sometimes crowded (Fig. 1e), superficial, at first orbicular with a narrow margin, expanding at maturity to

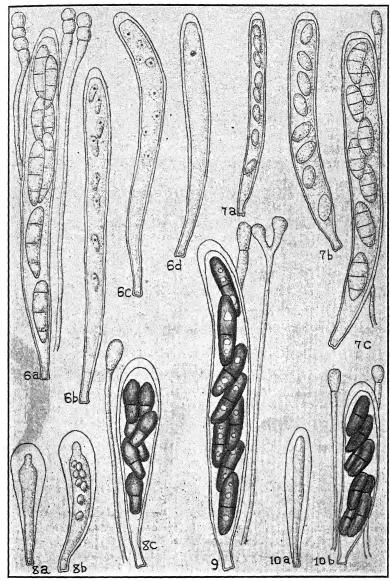


Fig. 6a. Paraphyses and mature ascus with spores of L. clavisporum; b-d, younger stages in ascus development. Fig. 7a, b. Development of the ascus of L. simile; c, paraphyses and mature ascus with spores. Fig. 8a, b. Development of the ascus of Karschia lignyota; c, paraphyses and mature ascus with spores. Fig. 9. Paraphyses and mature ascus of K. stygia. Fig. 10a. Young ascus of K. imperfecta; b, paraphyses and mature ascus with spores.

a diameter of 0.5-2 mm., round or slightly contorted by mutual pressure, immarginate, attached by a central point, shiny black. fuscous beneath, glabrous, carbonaceous, disc plane, becoming strongly convex and softened when moist: excipulum pseudoparenchymatous, composed of large hexagonal cells 15–33 u in diameter those toward the outside with thick, brown walls; hypothecium red-brown, about  $50 \mu$  wide, composed of small cells with thick red-brown walls, arranged parallel with the surface of the hymenium, and grading gradually into the excipulum (Fig. 2C): asci cylindric-clavate (FIG. 9), the wall thickened at the slightly narrowed apex, reaching a length of 50-75 (99)  $\mu$  and a diameter of 6-10  $\mu$ , 8 spored; spores irregularly biseriate, elliptic-subcylindric, often a little curved, guttulate, light brown, 15-20 u long by 4-6  $\mu$  wide; paraphyses numerous, filiform, branched and septate, enlarged above, tips colorless or brown, closely agglutinated with a brown extraneous substance forming a brown epithecium.

On Aleurites, Alnus, Carpinus, Liriodendron, Populus and Tilia. Type Locality: New Jersey and South Carolina.

DISTRIBUTION: Georgia, Indiana, Iowa, Massachusetts, Michigan, New Jersey, New York, Ohio, South Carolina, Virginia; Canada; Bermuda; Mexico; England; Germany; Italy.

Specimens examined: Bloxam, Sept. 17, 1856 (K); Twycross (K) Type of P. Bloxami; Brown, Britton & Seaver, Expl. Bermuda 1488 (N. Y.): Cavara, Fung. Longobardiae 116 (B, B. M., L, N. Y., V, W); Davidson, 733b (W); Dearness, 1097 (N. Y.); Fairman, Myc. Fairman 4528 (Cornell) Type of K. elaeospora; Fink, Porto Rican Fungi 2057 (N. Y.): 2057 (N. Y.); Fink & Fuson, Ascom. Ind. 188 (H); Gerard, 11 (N. Y.); Holway, 333 (N. Y.); Kauffman, 1910, Ann Arbor (N. Y.); Macoun, 405 (N. Y.); Kew Herb., N. J. 4590 (K, N. Y.) Cotype of K. stygia; Massee, N. J. 4500 (N. Y.); Morgan, 7 (N. Y.); 260 (N. Y.); 266 (N. Y.); 905 (N. Y.); Murrill, W. A. & E. L., Fungi Tepite Valley 524 (N. Y.); 457 (N. Y.); Peck, Portville, N. Y. 1059 (A, K, N. Y.) Type of P. fusispora; 133 (K); Rabenhorst, Fung. Eur. 1152 (B, Br, G, K, N. Y., V); Ravenel, Car. Inf. 3911 (K) Cotype of K. stygia; Saccardo, Myc. Ven. 1201 (K, N. Y.); Treviso (B, K) Type of K. nigerrima; Schweinitz Herb., "Patellaria difformis" (K); Seaver, Iowa Fungi 87a (N. Y.); Shimek, 43 (N. Y.); Thaxter, Farlow Herb. 1023 (H); 670 (H); Thompson, Univ. Toronto Herb. 2058 (N. Y.).

The three specimens reported by Berkeley and Curtis in the original description of the species, were examined in the herbarium at Kew and are considered type material. One of them (Sprague 6234) is not K. stygia but is K. lignyota. The other two (Ravenel 3911 and New Jersey 4590) agree with the type description.

Specimens of K. nigerrima Sacc. from the type collection on Alnus in Treviso were examined at Kew and Berlin, and found to be identical with K. stygia. The type of K. fusispora was examined in Peck's Herbarium at Albany and it agrees in all respects with K. stygia. No specimen of K. Taveliana Rehm could be found in Rehm's Herbarium in Stockholm, but material in The New York Botanical Garden Herbarium collected by Seaver in Iowa and identified by Rehm as K. Taveliana is the same as K. stygia. This is considered sufficient evidence, since Rehm's original description of the species is also in perfect agreement with K. stygia, to place the species in synonymy here. The type of P. Bloxami Berk. in Berkeley's Herbarium at Kew was examined, and although the spores seem more broadly elliptical than is typical of K. stygia, as it was the same in all other characters, it is considered a synonym of K. stygia.

Karschia elaeospora Fairman is apparently known only from the original collections. The type specimen was sent to me for examination from the herbarium of Cornell University through the courtesy of W. L. White. The material is extremely fragmentary. It seems to be the same as K. stygia, although the two apothecia that appear mature are small, and the spores are shorter, averaging only  $13~\mu$  in length. The red-brown hypothecium and large celled excipulum are typical of K. stygia.

This species is easily distinguished by the large apothecia, attached at a central point, and in section by the red-brown hypothecium and the conspicuous, hexagonal cells of the excipulum.

Karschia Lignyota (Fries) Sacc. Syll. Fung. 8: 779. 1889.
 Pesiza (Patellea) lignyota Fries, Syst. Myc. 2: 150. 1822.
 Patellaria lignyota Fries, Summa Veg. Scand. 366. 1849.
 Arthonia melaspermella Nyl. Flora 48: 605. 1865.
 Karschia Strickeri Koerb. Parerg. Lich. 460. 1865.
 Patellaria Strickeri Sacc. Michelia 1: 57. 1879.
 Poetschia Strickeri Stein in Cohn Krypt.-Fl. Schles. II. 2: 224. 1879.

Karschia nigricans Rehm, Ber. Nat. Ver. Augsburg 26: 10. 1881.

Karschia sphaerioides Ellis & Ev. Proc. Acad. Phil. 453. 1893.

Apothecia scattered or slightly crowded (Fig. 1f), superficial, globose, at first with a conspicuous incurved irregular margin, expanding to a diameter of 0.3-1 mm., typically patelliform with the margin almost disappearing when mature, flat and sessile, brown-black when young, becoming black with age, smooth, cartilaginous, softening when moist, disc plane; excipulum about 10 µ wide, pseudoparenchymatous, composed of hyphae with thick brown walls; hypothecium about 50 μ wide, yellow-brown in color, gradually grading into dark brown pseudoparenchyma at the base, with numerous brown-black hyphae spreading from the base into the substratum; asci broadly clavate (FIG. 8), with the wall greatly thickened at the rounded apex, tapering beneath to a short stipe, reaching a length of 25-45 (55)  $\mu$  and a diameter of 10-14  $\mu$ , 8 spored; spores irregularly arranged, ovate-oblong, 2 celled, slightly constricted at the septum, the upper cell a little wider than the lower, blunt or slightly narrowed at the apex giving a characteristic slipper shape, with a large oil drop in each cell, 8–12 (16)  $\mu$  long by  $4-5 \mu$  wide; paraphyses numerous, filiform, branched above, septate, the enlarged tips colored brown and closely agglutinated forming a heavy epithecium above the asci.

On Abies, Acer, Betula, Carpinus, Hypoxylon, Nyssa, Ostrya, Quercus, Ulmus; Polyporus; thalli of Biatorina pineti and Microphiale diluta.

Type locality: Europe.

DISTRIBUTION: Alabama, Florida, Michigan, New Hampshire, New Jersey, New York; England; Germany; Italy; Switzerland.

Specimens examined: Commons, 1338 (N. Y.); Earle, Alabama Biol. Surv. 12/10/99 (N. Y.); Ellis, N. Am. Fungi 400 (A, B. M., H, K. N. Y.); 1064 (N. Y.); 3022 (K, N. Y.); Newfield, N. J. March 26, 1893 (N. Y.) Type of Karschia sphaerioides; Farlow, Chocorua, N. H. Sept. 28, 1907 (H, N. Y.); Holway, 364 (N. Y.); Morgan, 33 (N. Y.); Phillips, Elv. Brit. 146 (B, E, K, N. Y.); Plowright, 1064 (N. Y.); Ravenel, Car. Inf. 1224 (K); Rehm, Ascom. 21 (K, N. Y., V); Roumeguère, Fung. Sel. Exs. 7350 (G, N. Y.); Smith, H. & A., 6197 (N. Y.); Sprague, 6234 (K); Wehmeyer, 212 (N. Y.).

This species is readily distinguished by the characteristic yellow green color of the hymenium in section, and by the slipper shape of the spores. An examination of the type specimen of K. sphaerioides Ellis & Ev. showed that it is identical with K. lignyota. The margins of the apothecia are no more strongly incurved than is typical for K. lignyota.

It is interesting to note that mycologists and lichenologists have disagreed as to the classification of *K. lignyota*. As Currey said: "It is a doubtful plant, which seems to hover between the fungi and lichens." Lindsay (25) said: "It has equal claim to be considered a lichen or fungus." Nylander placed it with the lichens, while Rehm considered it a fungus. As it occurs either as a saprophyte on wood or as a parasite on lichens, Keissler (21, p. 201) considered it a facultative lichen parasite.

3. Karschia imperfecta (Ellis) Sacc. Syll. Fung. 8: 782. 1889. Patellaria imperfecta Ellis, Bull. Torrey Club 8: 74. 1881.

Apothecia scattered (FIG. 1g), superficial, globose when young with a slight brown margin, expanding to a diameter of 0.3–0.5 mm. at maturity, orbicular, immarginate, sessile, disc plane, black, smooth, or frequently dimpled in the center, carbonaceous, becoming soft when moist and strongly convex; excipulum pseudoparenchymatous, composed of hyphae with thickened light brown walls; hypothecium about 25  $\mu$  wide, red-brown in color; asci cylindric oblong (FIG. 10), the wall thickened at the rounded apex, reaching a length of 24–39  $\mu$  and a diameter of 7–12  $\mu$ , 8 spored; spores biseriate, elliptic-cylindric, 2 celled, not constricted at the septa, 8–13  $\mu$  long by 3  $\mu$  wide, red-brown in color; paraphyses filiform, septate, with enlarged brown tips united into an epithecium above the asci.

On old corn stalks.

Type locality: Newfield, New Jersey.

DISTRIBUTION: Known only from the type locality.

Specimens examined: *Ellis, 1057* (N. Y.) Type; on old corn stalks Oct. 1879 (N. Y.); Aug. 27, 1880 N. J. (N. Y.).

This species was collected in two successive years from the same locality. It is distinguished from K. lignyota by the shape of the spores, the red brown hypothecium, and paler excipulum as well as by the immarginate mature apothecia.

### DOUBTFUL AND EXCLUDED SPECIES

Karschia crassa Fairman, Jour. Myc. 10: 229. 1904.

The type specimen, Fairman no. 1977, collected in Lyndonville, N. Y., was sent to me from Cornell University. It is very fragmentary, but seems to agree with *Buellia myriocarpa* (Lam. & DC.) De-Not., which

according to Zahlbruckner (50) is the same as *Buellia punctata* (Hoffm.) Massal.

Karschia impressa Ellis & Ev. Bull. Torrey Club 24: 470. 1897.

This species is known only from the original collection made by Bethel in the San Juan Mountains of Colorado, on living stems of Symphoricarpus. It was distributed as Bethel no. 356, and in the Morgan Collection as no. 1227. In external appearance it is very like Karschia, although the surface is strongly papillate, a condition not typical for this genus. In cross section the asci are found to be grouped in separate locules, not in a continuous hymenium with paraphyses. The asci are cylindric-oblong, abruptly narrowed at the base, short stipitate,  $40-55~\mu$  long by  $8-14~\mu$  wide. The spores are arranged irregularly, ovate-oblong, 2 celled, with the septum nearer the apex, colored a pale yellow-brown,  $8-13~\mu$  long by  $4-5~\mu$  wide. This fungus does not belong in the genus Karschia. It probably should be placed in the Dothideaceae.

Karschia occidentalis Earle in Greene, Pl. Baker. 2: 8. 1901.

A portion of the type collection on *Juniperus* from Hermosa, Colorado, was examined in the herbarium at The New York Botanical Garden. It is the same as *Buellia punctata* (Hoffm.) Massal.

Karschia patinelloides (Sacc. & Roum.) Sacc. Syll. Fung. 8: 780. 1889.

The original collection by J. Therry, as distributed in Roumeguère's Fung. Gall. Exs. 1075 is the same as Buellia punctata (Hoffm.) Massal.

Karschia Pertusariae Vouaux, Bull. Soc. Myc. Fr. 29: 453. 1913.

This species was known from Mexico only, but Keissler (21, p. 187) found in the herbarium at Uppsala a specimen collected in Sweden. I have seen no material of this species, but Keissler considers it a valid species. It grows on the thallus of Pertusaria.

Karschia Ricasoliae Vouaux, Bull. Soc. Myc. Fr. 29: 448. 1913.

A new species, growing on the thallus of *Ricasolia*, reported from Mexico. No specimens have been available for study.

Karschia Sabinae (De-Not.) Rehm, Hedwigia 21: 115. 1882.

Tryblidium sabinum De-Not. Comm. Soc. Critt. 2: 491. 1867.

In 1896 Rehm (17) placed this species in the genus Caldesia Trev., in the Pseudopatellarieae. He was using the name Caldesia in a new and entirely different sense from that of Trevisan. The species Trevisan had included in Caldesia belong in Melaspilea or Arthonia. Rehm was uncertain of the relationships of Caldesia Sabinae, and in 1912 (37) transferred it to the Cenangiaceae. Saccardo (41) included this species in the Hysteriaceae and later (42) in the Patellariaceae. In 1918 von Höhnel (20) made Caldesia, in the sense of Rehm, a synonym of Eutryblidiella Rehm (36), and the new combination Eutryblidiella sabina (De-Not.) Höhnel in the Tryblidiaceae. Clements and Shear (8, p. 311) placed Caldesia (Trev.) Rehm em. in the Tryblidiaceae and Nannfeldt (30, p. 334) made Caldesia Rehm (non Trev.) a synonym of Tryblidiella in the Lecanorales.

This species was first collected in this country by C. F. Baker in Hermosa, Colorado, on *Juniperus*. The apothecia are scattered, erumpent, black, carbonaceous, globose and closed at first, then opening irregularly, usually by lobes, the margin persistent. Excipulum composed

of small dark brown heavy walled cells, the hypothecium very thick. The asci are thick walled. The spores are 2 celled, brown. These characters of the apothecia separate the species from *Karschia*. It will be interesting to check the type of ascus dehiscence in fresh material. The species is without doubt closely related to *Tryblidiella rufula*.

Karschia Trypethelii (Tuck) Keissler, Ann. Nat. Mus. Wien 41: 168. 1927.

Buellia Trypethelii Tuck. Syn. N. Am. Lich. 2: 106. 1888.

Buelliella Trypethelii Fink, Lich. Fl. U. S. 372. 1935.

Tuckerman's type for this species was a specimen growing on the thallus of *Trypethelium carolinianum*, collected in Florida by A. H. Curtis. Keissler on the basis of material collected in Florida by S. Rapp, and agreeing with the original description, transferred the species to the genus *Karschia*, saying it is closely related to *K. advenula* Zopf. Fink placed it in his genus *Buelliella*. No material has been available for study, but according to the descriptions I believe it should be called *Buellia Trypethelii* Tuck.

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